THE EXPERIMENTAL TAXONOMY OF *CAMPANULA ROTUNDIFOLIA* L.

by

HUGH A. McALLISTER

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NOMENCLATURE AND TERMINOLOGY

The nomenclature used throughout the thesis is that of Flora Europea (Tutin et.al 1964-) and Clapham et.al (1962) for vascular plants, and Warburg (1963) and Paton (1963) for bryophytes. In Campanula (for which the final Flora Europea account is not yet available) the nomenclature follows the most recent taxonomic works (Podlech 1965, Kovanda 1970c). In table 3.8 the authorities of all the Campanula species mentioned in this thesis are given.

In the description of populations the deme terminology has been used because of the precision of its terms (Gilmour and Heslop - Harrison 1954). The terms most frequently used are:-

cytodeme - a group of plants sharing some cytological feature (e.g. chromosome number)

topodeme - (cf. population) a group of plants growing in a particular locality

phenodeme - a group of plants having a particular appearance

CHAPTER 1 INTRODUCTION

SECTION 1 - INTRODUCTION

A close examination of almost any plant species reveals a certain degree of variability which may not be immediately obvious from the descriptions in floras. Variation may be morphological, cytological, biochemical, physiological, ecological, etc., or any combination of these. There are perhaps two different approaches to the experimental study of variation. Firstly there are extensive studies involving extensive collecting, and concerned with the basic widespread pattern of infraspecific variation and variation at the species level. Such studies are often concerned largely, but not exclusively, with taxonomic issues and evidence for the evolution of species, and take what is termed the experimental taxonomic or biosystematic approach. Secondly there are intensive studies which are more concerned with small scale variation at the population (=topodeme) level. Here attention is focused on gene frequency changes at the basic Mendelian population level. The study of variation at this level is termed genecology.

In any particular species group extensive studies usually precede intensive research. For example Bradshaw's (1959) early work on Agrostis tenuis was based on extensive collections, while more recent work by himself, McNeilly, and Antonovics (Antonovics 1968a, 1968b, McNeilly and Antonovics 1968, McNeilly and Bradshaw 1968) involved studies on small collections carefully made for specific purposes.

The work described in this thesis is the result of an extensive survey of the variation in Campanula rotundifolia in the British Isles. As I shall show, although a certain amount of work has been carried out on the Continent of Europe, only limited information is available on the variation in this species in the British Isles.

SECTION 2 - THE BASIC APPROACH IN THIS WORK

Although in general an extensive experimental taxonomic approach has been taken in this work, detailed studies have been made in certain areas. Despite the fact the work was primarily concerned with the British Isles, material from abroad was obtained for comparison.

In making the collections the first object was to obtain material from a wide geographical area, and particularly from all parts of the British Isles, to determine which taxa and cytodemes were present. Once this had been achieved and the geographical distributions of the separate entities worked out, more detailed work could commence on the comparative morphology, ecology, breeding system, population biology and interbreeding relationships.

SECTION 3 - THE CHOICE OF CAMPANULA ROTUNDIFOLIA

A brief review of the literature on C.rotundifolia will now be given to indicate why it was considered that a study of this species in the British Isles would be rewarding. This is not intended to be a thorough survey of the literature, but only to indicate the background against which this thesis was planned. Full reference to the available literature is given in each chapter.

(a) Taxonomic variation

As described in the standard British Flora (Clapham et al. 1962) C.rotundifolia (fig.1.1) is an easily distinguished species of dry habitats. The distinguishing features are the blue, bell-shaped flowers borne on thin pedicels, and the marked heterophylly. The basal rosettes bear rotund to heart-shaped leaves from whose axils most of the flowering stems arise. These stems bear ovate to lanceolate leaves towards the base which merge into more linear leaves as one passes upwards towards the inflorescence. In the subsection of the genus Campanula to which C.rotundifolia belongs forty nine species have been described from the European mainland and North Africa, yet

a	b	c
48.8 (2x)	3.8(4x)	91.8(6x)
East Germany	Argyll	Mull, Argyll

FIG. 1.1 C.rotundifolia

Diploid, tetraploid and hexaploid specimens of C.rotundifolia

only C.rotundifolia is described as native in British floras. In addition to the species described from Europe, a few others - about three, but the exact number depending on the taxonomic concepts of the various authors - occur in other temperate and arctic regions of the Northern Hemisphere.

Although only C.rotundifolia is usually accepted as native in Britain there are three published records of C.gieseckiana (Hruby 1930, Podlech 1965) from the British Isles and several more herbarium specimens so named by Podlech. Clearly one of the first tasks was to carry out a careful examination of herbarium material from all parts of the British Isles, and to compare this with material of the described continental species. This classical type of taxonomic research would, it was hoped, update the taxonomy of British C.rotundifolia.

(b) Cytological variation

In Europe four cytodemes have been reported, namely diploids (2n=34), triploids (2n=51), tetraploids (2n=68), and hexaploids (2n=102) (fig. 1.2) (Böcher 1960, Gadella 1964, Kovanda 1966c, 1970a). Pentaploids have been produced in cultivation (Gadella 1964). Both diploids and tetraploids have been reported with B- chromosomes (Böcher 1960; Kovanda 1970a). It has been reported by Böcher (l.c.) that diploids of C.rotundifolia s.s. occur primarily in the lowlands of Central Europe, though he does describe a diploid topodeme from the Alps. Tetraploids are widespread, especially in areas glaciated during the last Ice Age. Hexaploids are scattered and rare.

There are only a few published chromosome numbers for British C.rotundifolia (fig. 1.2). Kovanda (1966b) reported diploids in three sites in eastern Britain (Berwick-on-Tweed, Downham Market in Norfolk, and Cambridge), and Böcher (1960), as a result of pollen grain measurements, forecast that they would be found on the Isle of Wight. Tetraploids have been described from Scotland, northern England, and northern Ireland (Böcher 1960, Gadella 1964), and Morriset (pers.

FIG. 1.2 Known distribution of cytodemes of C.rotundifolia and C.gieseckiana before the beginning of the work on this thesis (after Böcher 1960, Gadella 1964, Laane 1968).

○ = diploids

● = tetraploids

△ = hexaploids

comm.) has discovered hexaploids at the Lizard, and in the Galtee Moutains in Southern Ireland.

Several authors (Böcher 1960, Laane 1968) point out that there are two diploid taxa in northern Europe. One, C.rotundifolia, occurs in lowland continental areas and the Baltic islands, often, but not always, in areas which remained ice-free throughout the last glaciation. The other, C.gieseckiana ssp. gieseckiana, has been found in north Norway in presumed glacial refugia. Thus it was considered that while it was probable that the former occurred throughout southern and eastern England, the latter might be found in the mountains of north Britain. It was anticipated, however, that the tetraploid would be the commonest cytodeme throughout most of the country, although Morriset's hexaploid counts suggested that further hexaploid populations might be found in south-western parts of the British Isles, particularly the West Country, and the southern parts of Ireland.

As C.rotundifolia appears from the distribution map to have a more or less continuous distribution throughout Great Britain (fig. 1.3), there was the likelihood of finding hybrids where two chromosome races met. Such hybrids are reported to be easily made in cultivation (Gadella 1964), but have rarely been detected in the wild. (Gadella l.c., Kovanda 1966c).

Before the beginning of this work sufficient was therefore known to suggest that an interesting cytological pattern would emerge from a study of British material.

(c) Morphological variation

The primary aim of most previous work on the morphology of the C.rotundifolia complex has been taxonomic (Böcher 1960, 1966, Gadella 1964, Kovanda 1970a). Within C.rotundifolia s.s. and C.gieseckiana attempts have been made to separate the cytodemes morphologically. It has never proved possible to find characters which will do this in every case, but Böcher (1960) found

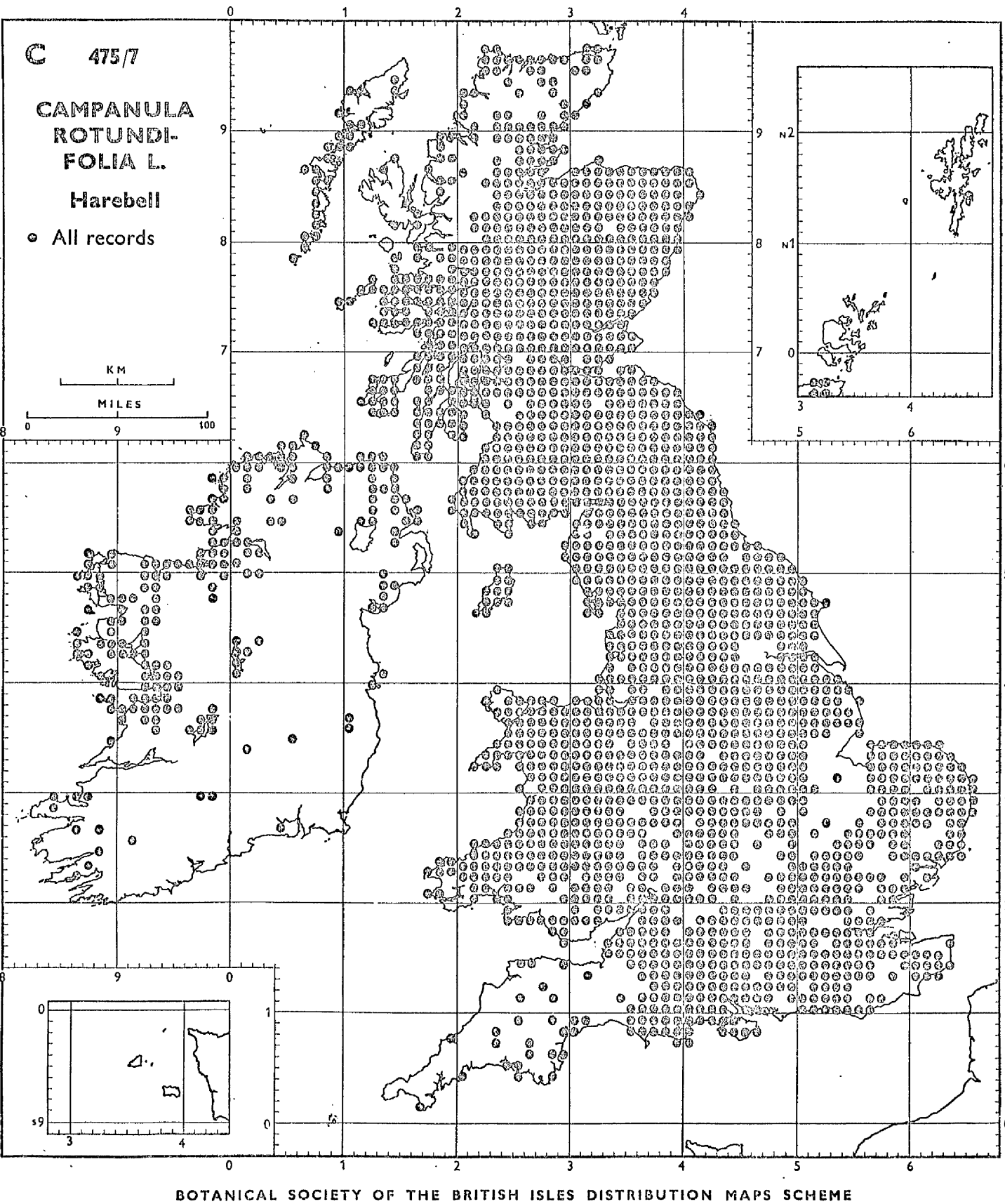


FIG. 1.3 The distribution of C.rotundifolia in the British Isles

sufficiently reliable methods in C.gieseckiana to be able to describe the two cytodemes as separate subspecies.

In my own studies I intended to make observations on the morphology to see if it would be possible to distinguish the cytodemes within the British Isles, though I felt that the variation present was worthy of study for its own sake. I also planned to examine the variation that could be induced between ramets of a clone by growing them in contrasting environments.

Turesson (1922, 1925, 1930) found considerable genecological differentiation between lowland and high altitude and high latitude plants, and I planned to look for such variation within the British Isles.

(d) Ecology

Preliminary observations showed that C.rotundifolia appeared to be a calcicole in western Scotland, whilst in eastern parts of the country it seemed to have a much wider habitat range, occurring in acid heather moors as well as calcareous situations. It therefore seemed worthwhile to carry out a survey of the habitats occupied by C.rotundifolia in different parts of its range, particularly in relation to the different cytodemes.

(e) Reproductive biology

Although there was a certain amount of information in the literature on the pollination biology and breeding system of the species, little work could be traced on other aspects of its reproductive biology. It was therefore decided to study the breeding system and all aspects of seed production, dispersal, germination and seedling establishment. From this study it was hoped to make some assessment of the relative importance of vegetative and sexual reproduction in the species. In the same context, it was planned to examine, in morphological terms, how a seedling developed, and at what stage it bore flowers and began producing rhizomes. This study of chronological development would give information which might make it possible to age young plants in the wild.

The breeding system however was to come under special study because of the conflicting reports in the literature. While polyploid derivatives are often somewhat self-compatible, related diploids are frequently totally self-incompatible (Fryxell 1957). However, Gadella's (1964, p.62) attempts to self tetraploids and hexaploids of C.rotundifolia were unsuccessful, and Block (1964) believed tetraploid C.rotundifolia to be almost totally self-incompatible. On the other hand Bielawska (1964, 1968), working with Polish tetraploids, found most genotypes to be at least slightly self-compatible, although diploid C.cochleariifolia was self-incompatible. Only a few plants were used in these experiments and I intended to repeat them using a larger number of plants.

(f) Geographical considerations

The distribution map of C.rotundifolia in Britain (fig. 1.3) revealed some odd features. The rarity of the species in Ireland was the most striking, although absence from the West Country, the Wash, and inland north-west Scotland also required consideration. The intensive arable cultivation practiced in the area round the Wash may leave few habitats suitable for C.rotundifolia, but the other absences did not seem to have any ready explanation. Ireland in particular is not vastly different from many areas of lowland England.

These features would have to be considered in the light of the distribution of the cytodemes as that became known.

As already mentioned Böcher (1960) and Laane (1968) remark on the occurrence of diploids primarily in areas unglaciated in the last Ice age, while tetraploids are found in formerly glaciated areas. Thus it was thought profitable to study the distribution patterns of the cytodemes in relation to glacial and post-glacial geomorphology. From the subfossil record (Godwin 1956) it seemed probable that C.rotundifolia had been present in Britain since at least the last (Weichselian) full glacial period.

(g) Hybridisations

Although natural and synthetic hybrids are said to be rare in the genus Campanula (Crook 1951), Gadella (1964) and Bielawska (1964, 1968) reported relatively high interfertility between certain taxa close to C.rotundifolia and C.rotundifolia itself, and between the different cytodemes of C.roturdifolia. I therefore planned to make crosses between plants of the one cytodeme from widely separate localities, as well as to try to cross the different cytodemes and plants of different named taxa.

(h) Foreign material

Finally, material collected outwith the British Isles would be considered in relation to the described taxa and the observations on British material. This it was hoped would enable tentative conclusions to be drawn regarding the evolutionary relationships of British plants.

SECTION 4 - SUMMARY OF OBJECTIVES

In summary the major aims of the study were:-

1. To discover which taxa are present in the British Isles (Chapter 3);
2. To discover which cytodemes of C.rotundifolia are present in the British Isles, and to work out their distribution (Chapters 4 and 8);
3. To describe the morphological variation of British material and to try to discover characters to distinguish the cytodemes (Chapter 5);
4. To study the autecology and reproductive biology of C.rotundifolia (Chapter 6 and 7);
5. To investigate the intercrossability of plants of the same cytodeme but from different geographical areas.
   To investigate the intercrossability of plants of different cytodemes (Chapter 9);
6. To examine the relationship of British material to foreign collections (Chapter 10);
7. Using the data available, to discuss the variation and evolution of the C.rotundifolia group of species (Chapter 11).

CHAPTER 2: COLLECTION AND CULTIVATION OF MATERIAL

SECTION 1 - INTRODUCTION

The primary object of the study was to make a general survey of C.rotundifolia in the British Isles, to discover which cytodemes are present and to work out their distributions. Hence collecting was extensive, covering all areas of Britain, rather than intensive within a small area. Almost all the material collected was cultivated to obtain root-tips for cytology and for morphological examination. As a result of the impressions gained from the preliminary observations, certain genotypes (including both typical and extreme variants) were selected for more detailed morphological study (Chapter 5).

SECTION 2 - COLLECTION

(a) Choice of sites

As one major object of the project was the study of the cytological variation of C.rotundifolia s.l. in the British Isles, it was planned to collect from many sites. Being based in Glasgow, and in view of the fact that "The Scots Bluebell" is considered something of a national flower, I hoped to collect extensively in Scotland, though the pattern of collecting would be largely influenced by indications of where interesting specimens might be found.

The map giving the British localities of cytologically known material (fig. 1.2) suggested that three cytodemes were found in Britain. Letters requesting material were sent off to friends living in distant parts of the British Isles. Several collecting trips were also made in Scotland, Ireland and England. The early discovery of hexaploids in the Oban area, and the receipt of very distinctive large flowered herbarium specimens from the Outer Hebrides, quickly turned my attention to the west coast of Scotland. A steadily increasing number of hexaploid counts from western localities soon made Böcher's records of tetraploids from the west of Ireland (Böcher 1960)

look out of place, and necessitated the collection of material to confirm or refute his findings.

Although there was no published evidence that diploids might be found in northern areas of Scotland, there presence in North America (Löve and Löve 1965), Greenland (Böcher l.c.), and north Norway (Laane 1968) suggested that there was just a possibility that they might turn up in association with arctic-alpines in relict mountain sites. Such localities were visited whenever the opportunity arose. At first only tetraploids were found, but the eventual discovery of hexaploids on Ben Nevis gave the collection of mountain material a new urgency.

Collecting trips were also arranged to the European mainland and Iceland. In 1967 I was able to make a fairly extensive collection from the Picos de Europa region of the Cantabrian Mountains in Northern Spain, and an expedition to Iceland in 1971 yielded another large foreign collection. Through correspondents I obtained material from East and West Germany, Austria, Morocco, Greenland, Newfoundland, the Isle Gaspé in the St. Lawrence estuary, Lake Superior, and Alaska.

Though largely fortuitous, the choice of foreign collecting sites turned out to be a very happy one. The Greenland material, referable to C.gieseckiana (Böcher 1960), allowed comparison between that species and C.rotundifolia. Extensive Icelandic collections enabled me to come to some tentative conclusions about the relationship of the Icelandic harebell to C.gieseckiana and C.rotundifolia - the occurrence of the latter species in Iceland has been considered problematical (Kovanda 1970c). The collections from Northern Spain gave me representatives of material which was later to be named C.asturica and C.wiedmannii (Podlech 1970), the two most recently described species in the series Vulgares.

(b) Sampling

In most instances living plants were collected, largely because much of

the collecting was done at times when seed was not available. Also, as has been pointed out by Heslop-Harrison (1964), there are major objections to using material grown from seed in genecological work. Seed was however collected whenever it was available in case the living plants did not survive - which rarely happened.

The sampling method used at any particular site depended upon the distribution of the species in the area. This varied from scattered individuals on mountain cliffs or roadsides, to large populations where the boundary between presumed clones was impossible to determine. Where the population consisted of a few isolated individuals ramets were taken from a few plants, an attempt being made to include each clone only once by spacing the samples as widely as possible. On a cliff, only one plant was taken from each ledge, and in a grassland only one from each patch. Any obvious morphological variants were also collected. In larger populations the most extreme morphological forms were always collected, as well as the plants more typical of the population.

This great care in sampling was necessary as it has been shown in several species (Smith 1965 in Festuca rubra, and Harberd (1963) in Trifolium repens) that rhizomatous spread can result in a single clone being distributed over a very wide area. Work by Harberd (l.c.) on Trifolium repens suggested that in a variable species small differences in morphology between clones make the subjective separation of clones in the field a fairly reliable procedure for a careful observer.

Initially I intended to sample the vegetation at the site of each collection by means of a standard quadrat, denoting cover-abundance by domin numbers. However, it soon became obvious that in only a very small number of sites could such a quadrat method be used, most Campanula rotundifolia in western Scotland and Ireland occurring on cliff ledges or other such habitats

in which the environment changes over very short distances. Even where Campanula rotundifolia occurred in an apparently uniform vegetation-type, such as grassland or heather moor, closer inspection usually revealed that the plants only grew in particular places, e.g. in grassland, only on the bank of a stream where erosion was taking place, or over a boulder where the soil was particularly thin; or in a heather moor, only in a flush.

Ecological data was gathered for each plant I collected, though such information was rarely available for populations sampled by other people. The sampling sites were localised as accurately as possible (Six figure Grid Reference). The altitude, aspect and degree of exposure of the habitat were also recorded, together with comments on the surrounding vegetation. At the same time the frequency of C.rotundifolia in the locality was noted with observations on grazing pressure, the presence or absence of seedlings, and any other factors of importance.

As C.rotundifolia rarely forms pure stands, except perhaps in rock crevices, a turf containing the rhizomes was collected and taken back to the laboratory. There the turf was dissected, the rhizomes of C.rotundifolia extracted and planted, and the associated species in the turf listed with notes on their frequency. Any flowering stems present were pressed for future reference. After all the C.rotundifolia rhizomes had been extracted, the soil from the rooting levels was air-dried and stored in aluminium cans for later analysis of their p.H. values and water holding capacities.

When in flower Campanula rotundifolia is of course very easy to find in the field. At other times, and in situations where it very rarely flowers (e.g. mountain summits and heavily grazed grasslands) it can be very difficult to find. However, unless wilted or frozen, any part of a Campanula rotundifolia plant will exude a milky latex if broken. In this it resembles almost all members of the Campanulaceae, the subfamily Cichorioideae of the Compositae, and the genus Euphorbia, but differs from almost all other members of the British flora. This exudation of a milky latex has been found to be a

very useful character for the confirmation of the identification of vegetative material of C.rotundifolia. None of the British species with which confusion is possible has a milky latex, and on the Continent problems are only likely to arise with other members of the Campanulaceae - e.g. C.arvatica in North Spain.

The following notes are the results of very careful study of the vegetative differences between C.rotundifolia and some species with which it sometimes grows.

The species met in this study which most resemble vegetative C.rotundifolia are Viola riviniana, Cardamine hirsuta, Bellis perennis, Prunella vulgaris, and Campanula arvatica. These five species are discussed below, together with the ways in which they differ from C.rotundifolia. C.rotundifolia, for comparison, has a slightly dentate leaf and is often minutely hairy (pilose), in addition to having the latex exudation.

Viola riviniana is perhaps the species most likely to be confused with C.rotundifolia. Its leaves are usually more heart-shaped, and crenate rather than dentate. On extraction from the vegetation in which it is growing, the single rosettes with much thicker and more rigid roots, and the lack of creeping rhizomes, make V.riviniana fairly easily distinguishable.

Cardamine hirsuta only resembles C.rotundifolia when in a very reduced, depauperate, or young stage, having only a single terminal leaflet per petiole. In this condition the leaf is virtually identical to a basal leaf of C.rotundifolia unless the characteristic coarse hairs of Cardamine hirsuta are present. These hairs are often absent in small plants. In the herbarium of the Botany Department at the Glasgow University there is even a specimen of flowering C.rotundifolia with some leaves of Cardamine hirsuta as its presumed basal leaves - probably collected because one leaf shows the beginnings of pinnation, and was no doubt thought to be an interesting variant of C.rotundifolia.

Several times I myself thought I had found the same interesting variation, but each time it proved to be a plant of Cardamine hirsuta. On extraction from turf the lack of rhizomes usually distinguished Cardamine hirsuta. Cardamine hirsuta might be thought to occupy much wetter habitats than C.rotundifolia, but it is on wet shady cliffs that depauperate forms of the two species occur together.

Trifolium repens. The evening nyctotropic form of this species with folded leaflets may resemble C.rotundifolia at a distance, and can therefore make C.rotundifolia very difficult to distinguish in grazed turf where both species are present. On closer examination the two species can of course be easily distinguished, but even when leaves are fully expanded, the presence of Trifolium repens in a sward, masks C.rotundifolia, and can often lead to erroneous conclusion that the latter species is absent.

Another species whose presence in quantity has the same masking effect as Trifolium repens, is Prunella vulgaris. Bellis perennis can also have a masking effect in the field like Trifolium repens and Prunella vulgaris, especially in relatively short grazed turf. Several times I have been sent specimens of Bellis perennis as C.rotundifolia.

Campanula arvatica. In the Cantabrian Mountains this species often occurs with C.rotundifolia. It is not heterophyllous, and the basal leaves are more sharply toothed than is usual in C.rotundifolia, but the local C.rotundifolia has relatively sharply toothed leaves. C.arvatica also exudes a milky latex if broken.

SECTION 3 - CULTIVATION

C.rotundifolia is a relatively easy plant to cultivate and propagate. Rhizomes collected in the wild were planted in 2-5 inch pots, (depending on the amount of material) in John Innes No.2, or U.C. (University of California Mix) No.2. soil. The latter was used in the replicated trial reported in Chapter 5. Both clay and plastic pots have been used, but I find plastic pots

preferable as they dry out less readily (the rhizomes are quickly killed by desiccation). For the same reason the U.C. mix with its high peat content, and consequently its high water holding capacity, is preferable to J.I. soils. J.I. soils are also highly variable due to variation in the quality of loam used, which can be anything from good turf loam to clay. The U.C. mixes, on the other hand are of relatively constant quality, consisting only of sand and peat with added fertiliser. They do, however, waterlog easily, and so require careful watering.

Once a plant had become established, it was transferred to a 6" plastic pot and kept as a stock plant in the greenhouse. Plants have been kept successfully in such pots for three years, the only attention required being watering and occasional weeding.

Occasional plants were left outside in their plastic pots, or planted in the rather heavy soil of Glasgow. In every case the plant suffered badly from waterlogging, and usually died during the winter.

In the greenhouse the main problems (apart from waterlogging and desiccation) were pests. Plants weakened by waterlogging were very susceptible to two root and rhizome eating grubs, those of the dipteran fly Sciara sp. and the weevil Otiorrhynchus singularis (L). These were by far the most troublesome pests as they often completely destroyed the underground parts of infected plants before their presence was detected, and such a plant could rarely be saved. Simply repotting and careful watering often saved slightly affected plants. Overall control was obtained by fumigation with malathione, which killed the adult stages and the Sciara grubs in the top inch or so of soil.

Greenfly Myzus ascalonicus Doncaster were also a frequent pest, but being above ground they were easily seen, and therefore very easily controlled by fumigation with malathione or pyrethrum dust.

The red spider mite Tetranychus urticae C.L.K. only became a really serious pest on relatively hairy plants, and in the highly protected conditions existing when plants were being brought into flower under lights and flowers

were enclosed inside pollination bags. They could not be exterminated, but were more or less controlled by a combination of spraying a powerful water jet on heavily infested plants, malthione fumigation, and "azide" smoke pellets. It was interesting to note that in the stock pots the red spider mite acted as a biological control against Stellaria media and Cerastium fontanum, which suffered more severly than the C. rotundifolia.

The rhizome gall insect Perissa trachelii Wachtl. was occasionally detected in the wild, but never seemed to survive in cultivation. The same type of gall was seen on the aerial parts of a plant in the axils of the lower stem leaves in a herbarium specimen in the British Museum - the galls were labelled as bulbils.

A nematode which destroyed the growing root apices was occasionally seen in root tip squashes. How much damage it caused is uncertain as I made no attempt to differentiate between the effect of its activities and the direct effect of waterlogging and desiccation on root tip mortality. It was possibly the causative agent of nodule-like structures found on the roots of some plants.

Occasionally plants would suddenly produce curled malformed leaves and stems. The condition usually affected all the shoots in one pot, and was presumably the result of viral infection. Infected plants soon recovered and the condition was never lethal.

SECTION 4 - CONCLUDING REMARKS

The cultivated samples were available for cytology, morphological study and crossing experiments, while the lists of associated species and the soil samples were retained for later analysis. The methods used in the cytology, ecology, and hybridisation studies will be described in the appropriate chapters.

CHAPTER 3: THE TAXONOMIC POSITION OF CAMPANULA ROTUNDIFOLIA AND RELATED SPECIES IN THE GENUS CAMPANULA.

SECTION 1 - INTRODUCTION

In Great Britain C.rotundifolia is by far the best known member of the genus Campanula and of the whole family Campanulaceae. There are, however, about 60-70 genera in the family and about 2,000 species, around 300 of which are assigned to the genus Campanula itself (Willis, 1966).

From the standard British flora (Clapham et.al.1962) C.rotundifolia would appear to be an easily distinguished species with there being no real chance of confusion arising between it and closely related species. As discussed in Chapter 1, many morphologically similar taxa have been reported from the Continent of Europe, and British material is known to be highly variable. Thus, before embarking on a discussion of the material studied in the preparation of this thesis, I consider it appropriate to outline the systematic position in order to see C.rotundifolia in its setting. First I shall relate the subsection to which it belongs, the Heterophylla, to the taxonomic subdivision of the family Campanulaceae. Secondly, the subsection Heterophylla itself will be discussed in detail, both its delimitation and its composition being considered. Finally the taxa which have been described from the British Isles, the evidence for their presence, and taxa which might be found will be discussed.

SECTION 2 - THE FAMILY CAMPANULACEAE

There seems to be some agreement about the division of the family Campanulaceae into three units. Bentham in Bentham and Hooker (1876) gives three tribes; Lobelieae, Cyphieae, and Campanuleae, while Schönland, in Engler and Prantl (1894), makes the same division, but calls the units subfamilies. His subdivision of the units containing the genus Campanula is given in table 3.1.

a

C.rotundifolia

b

C.scheuchzeri

c

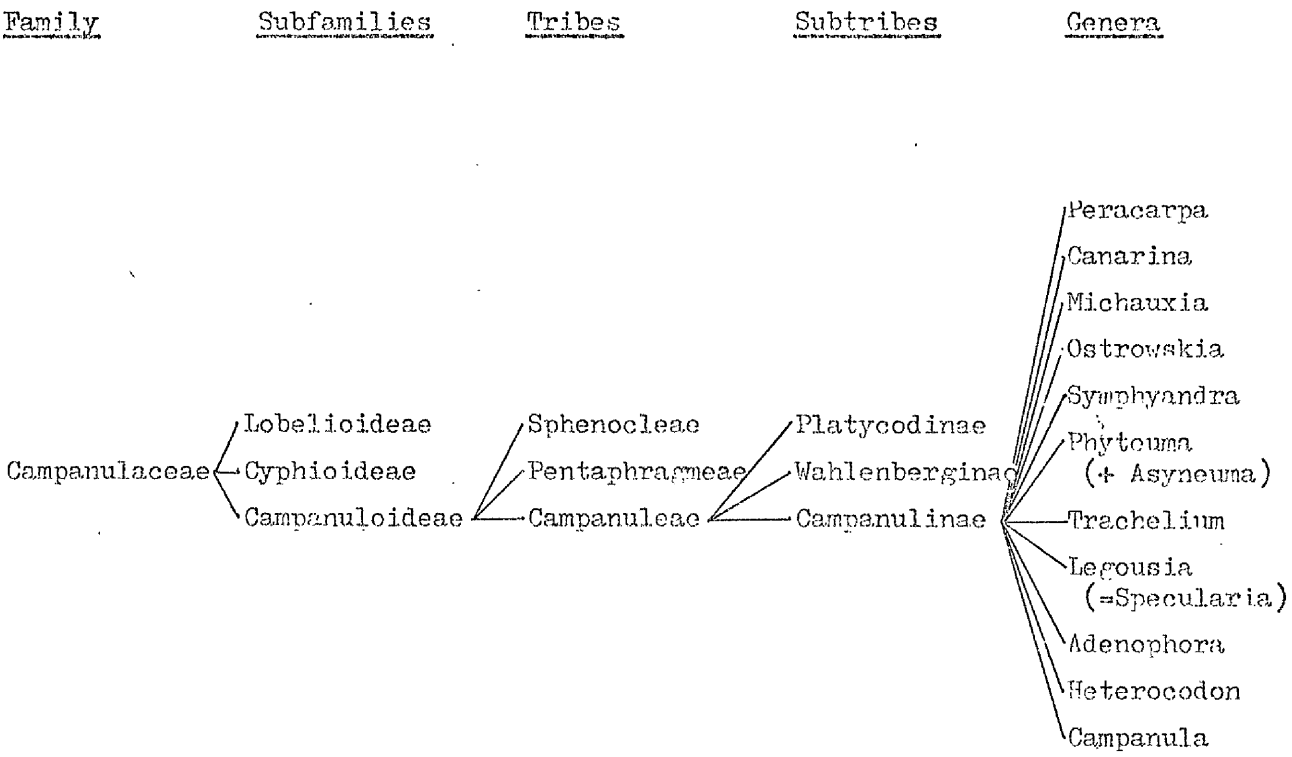
C.cochleariifolia

d

C.arvatica

FIG. 3.1

TABLE 3.1 THE SYSTEMATIC POSITION OF THE GENUS CAMPANULA IN THE FAMILY CAMPANULACEAE (AFTER SCHÖNLAND 1894)



Bentham divided the tribe Campanuleae into five groups, the fifth of which differs from Schönland's subtribe Campanulinae only in that Canarina and Peracarpa are placed in another group, and Heterocodon is included within Campanula. Many species now included in Specularia, Symphyandra, Adenophora, and Asyneuma, and in some of the genera of the other subtribes, were once included in the genus Campanula. Gadella (1964) remarks that certain species at present included in Campula bear more resemblance to species of these other genera than to other species of Campanula. These genera must therefore be considered in any work on the genus Campanula.

SECTION 3 - THE GENUS CAMPANULA

A. de Candolle (1830) has produced the sole monograph of the genus Campanula. He split the genus into two sections on the basis of the presence or absence of calyx appendages. Boissier (1875), dealing only with species from Greece, Egypt, and the Near East, also split the genus into two sections, but on the mode of dehiscence of the capsule. Nymann's classification (1878-1882) is similar to Boissier's, but divides the genus into three groups. The classifications proposed by these authors are presented in table 3.2, together with the definitive characteristics of the major categories.

Fedorov (1957) accepts Boissier's main subdivisions, Medium and Rapunculus, but then divides those up into a large number of subsections and series (Medium - 19 subsections; Rapunculus - 4 subsections), which he feels may be groups of phylogenetically related species. These groups are defined by character complexes rather than by single key characters. One of the nineteen subsections within the section Medium is the Heterophylla (Nym.) Fed., the group to which Campanula rotundifolia belongs.

TABLE 3.2 SUBDIVISIONS OF THE GENUS CAMPANULA ACCORDING TO VARIOUS AUTHORS

DE CANDOLLE SECTIONS	DEFINITIVE CHARACTERS	NYMANN GROUPS (Status undefined)	BOISSIER SECTIONS	FEDOROV (SECTIONS AS BOISSIER) SUBSECTIONS
MEDIUM Calyx appendiculate	Calyx appendiculate Capsule 5-locular Capsule valves basal	MEDIA Capsule 5-locular Capsule valves basal	MEDIUM Capsule valves basal	quinqueloculares Boiss. spinulosae (Fom) Fed. triloculares Boiss. phasidianthe Fed. tulipella Fed. dasystigma Fed. annuae (Boiss.) Fed. eucodon (D.C.) Fed. involucratae (Fom.) Fed. dictyocalyx Fed. cordifoliae (Fom.) Fed latilimbus Fed. trigonophyllym Fed. symphyandriformes (Fom.) Fed. oreocodon Fed. scapiflorae (Boiss.) Fed. rupestris (Boiss.) Fed. hypopolion Fed. heterophylla (Nym.) Fed.
	Calyx appendiculate Capsule 3-locular Capsule valves basal	CAMPANULASTRA Capsule 3-locular Capsule vales basal		
EUCODON Calyx non-appendiculate	Calyx non-appendiculate Capsule 3-locular Capsule valves basal			
	Calyx non-appendiculate Capsule 3-locular Capsule valves apical	RAPUNCULI Capsule 3-locular Capsule valves apical	RAPUNCULUS Capsule valves apical	campanulastrum (small) Fed. rotula Fed. melanocalyx Fed. odontocalyx Fed.

Gadella (1964, 1966) in two very useful papers, studied cytological as well as morphological characters in an attempt to define natural groups within the genus. Initially he hoped to be able to raise Fedrov's subsections to sectional rank. However crossing experiments suggested that some of Fedrov's groupings were unnatural, and Gadella described seven species groups defined morphologically and cytologically (table 3.3). In Gadella's opinion these groups can be regarded as natural, consisting of related species. A number of species do not appear to belong to any of the above seven groups, and should perhaps be placed in other genera. On the other hand, it is clear that species at present placed in the related genera, Symphyandra, Legousia, Asyneuma, and Adenophora may be very close to species included in Campanula, and these genera therefore require examination. The subsection Heterophylla belongs to Gadella's section VII.

Gadella points out the dangers inherent in using chromosome numbers in isolation to deduce relationships. From the ease with which they interbreed, and overall morphological and cytological (chromosome size) characters, he deduces that species with 2n = 30, 40, and 80 (x = 10) are unrelated to those with 2n = 30 and 90 (x = 15). Similarly, of the species with 2n = 32, only C.stevenii is related to other species with x = 8 (these have long chromosomes = 4-6 μm), the others (with short chromosomes = 2 μm.) probably being derived from species with 2n= 34 by reduction.

He also reviews the objections to the theories proposed to account for the origin of the base number x = 17. Tischler (1950) proposed amphiploidy, 2n = 16 x 2n = 18 $\Rightarrow$ 2n = 34, and Böcher (1960) polyploidy in a trisomic diploid with x = 8, (8+8+1) x 2 = 34. Gadella considers it is unreasonable to involve any known species with x = 8, as they have long

TABLE 2.2 SUBDIVISION OF THE GENUS PRIMULA

Group	x	2n	Comments and representative species	Chromosome size	Basal leaves cordate (+) non-cordate (-)	Longevity	Calyx appendages present (+) absent (-)	Style length / Stigma length	Style	Locule no.	Capsule position	Capsule dehisc
I	8	16 32	persicifolia steveni	LONG 4-6um	-	Perennial		1:1(2)	glabrous	3	erect	apical
II	10	18 20 40 80	Most of series rapunculiformes Fed. Annual rapunculus sensu Boiss.	MEDIUM 3-4um	-	Annual Biennial Perennial	-	5-8:1	hairy	3	erect	apical
III	13	26	peregrina	SHORT-MEDIUM 2-4um	-	Biennial	-	1:1	glabrous	3	erect	apical
IV	18	36	lactiflora primulaefolia	VERY SHORT <2um	-	Perennial	-	1:1	glabrous	3	erect	apical
V	12	24	dichotoma, most phasidianthe Fed.	SHORT 2(<3)um	-	Annual	+	7:1	hairy	3	not erect	basal
VI	14	24	erinus, colorata, cashmiriana	VERY SHORT <2um	-	Annual Perennial	-	6-10:1	hairy	3	not erect	basal
VII	17 15	30 90 34 68 102 43	Most species. No discontinuities. Not homogeneous. incl. heterophylla, quinqueloculares, spinulosae, triloculares, dasystigma, eucodon, involucratae, dictyocalyx, cordifoliae, latilimbus, scapiflorae, hypopolion rotula melandcalyx. odontocalyx.	SHORT <2um	-, +	Biennial Perennial	- +	5;10:1	hairy (one species glabrous)	3,5.	erect, not erect.	mostly basal. sometimes apical or medial

chromosomes, whilst those with x = 34 have short chromosomes. However species with x = 8 and short chromosomes may be found (Quézel 1957).

SECTION 4 - THE SUBSECTION HETEROPHYLLA (Witas.) Fed.

The subsection Heterophylla seems to be accepted by most authors as fairly natural, being distinguished from other species groupings primarily by the more or less distinct heterophylly, the cauline leaves being more elongate and less petiolate than the basal leaves (fig.1.1). Podlech (1965) states that the flowering stems arise from the axils of rosette leaves, not directly from the rhizome as in the isophyllous C.trachelium group. De Candolle (1830) recognised the Heterophylla, treating it as a unit in his classification. Podlech comments that C.herminii (2n = 32) is similar to some members of the Heterophylla, but can be excluded on the basis of its chromosome number (all members of the Heterophylla have x = 17). C.tommasiniana (2n = 34) and C.waldsteiniana (2n = 34), which are distinguished from the Heterophylla only by weak heterophylly and rhizome buds which grow out directly to flowering shoots, may form a link between the Heterophylla and the C.garganica-C.fragilis group. C.morettiana is also similar to some species in the Heterophylla.

The subsection Heterophylla is further divided by most authors (Krasan 1849, Witasek 1902, and Hruby 1930) (table 3.4).

Krasan, working on alpine species, recognised four groups, and was the first to refer to this collection of species as the C.rotundifolia complex. Witasek carried out a detailed study of many species belonging to three of the series, and Savelescu (1916) completed this subdivision by adding the series Pusillae. Hruby made a subdivision into seven groups which were left undefined.

WITASEK (1902), HRUBY (1930) AFTER KOVANDA (1970)	KRASAN (1894)	HRUBY (1930	SAVELESCU (1916) WITASEK (1902)	SPECIES AFTER FEDOROV (1957), PODLECH (1965, 1970), KOVANDA (1970a,b,c) BÖCHER (1960, 1966)
Thin root, thin rhizome, terete stem, erect buds, smooth ovary, anthers ≤ filaments, membranous pendant capsules, middle and N.European species with wide ecological amplitued	VULGARES	ROTUNDIFOLIAE	VULGARES	2x - gieseckiana ssp. gieseckiana, rotundifolia 4x - asturica, bohemica (=corcontica), gieseckiana ssp.groenlandica, intercedens, langsdorffiana, latisepa marchesettii, rotundifolia, wiedmanni 6x - bertolae, rotundifolia.
			vulgares / lanceolatae	cantabrica (2x), rhomboidalis (2x), baumgartenii (4x), beckiana (4x)
Thickened root, thin rhizome, angular stem, erect or pendant buds, smooth ovary, anthers ≥ filaments, membranous pendant capsule, meadow plants of south and mid-Europe.	LINIFOLIA	SCHEUCHZERICANAE	LANCEOLATAE	2x - precatoria, recta, serrata, witasecki 4x - gelida, scheuchzeri. 6x - ficarioides, polinensis, scheuchzeri.
		LANCEOLATAE		
			lanceolatae / saxicolae	gentilis (2x), romanica (2x).
Thickened root, thickened rhizome, terete stem, erect or pendant buds, Papillose ovary, anthers > filaments, lignose erect or pendant capsule. S.European rock plants.	FLACCIDAE	LINIFOLIAE	SAXICOLAE	2x - albanica, apennina, carnica, crassipe forsythii, gracillima, herceogovina, hispanica, justiniana, macrorrhiza, praesignis, ruscinonensis, sabatia, tanfani, xylocarpa. 4x - fritschii, hispanica, longisepala, moravica ssp. moravica, wilkomii. 6x - jurjurensis, moravica ssp. xylorrhiza
		BALCANICAE		
			saxicolae / vulgares	velebetica (4x), pseudostenocodon (6x)
Thin root, thin rhizome, terete stem, pendant buds, smooth ovary, anthers ≤ filaments, membranous pendant capsule. Mountain plants.	ALPICOLAE	CAESPITOSAE	PUSILLAE	2x - caespitosa, cochleariifolia, excisa, jaubertiana, pulla, stenocodon.
		PUSILLAE		

It can be seen (table 3.4) that there is a fair measure of agreement between the three classifications. A few species are, however, treated differently by different authors, e.g. C.polymorpha is included in the Scheuchzericanae of Hruby, but placed in the Vulgares by the other authors. Several species, as indicated, are intermediate between the sections, and cannot therefore be rightly placed in any. In Podlech's opinion these sections cannot be recognised taxonomically, because the distinguishing characters are combined in a net-like fashion, resulting in too many species having the key characters of several groups - e.g. C.rotundifolia, most characteristic member of the Vulgares, includes plants from southern Europe which have papillose ovaries - a character of the Saxicolae (Kovanda 1970). Podlech, unlike Fedorov (1957), rejects any classification in series, describing each species separately, but placing related species close together.

The Heterophylla is a fairly well defined subsection which, it is anticipated, would be little altered in its species composition by further work. C. rotundifolia is the most characteristic species of the subsection. This being the case, it can fairly safely be assumed that any species very closely related to C.rotundifolia s.s. will be included in the Heterophylla, and that there is no need to look outside this subsection in a study of this species. However, Bielawska (1964) has shown that C.cochleariifolia (fig. 3.1, table 3.6) a member of the distinct and well defined series Alpicolae, can, at least under experimental conditions, cross with tetraploid C.rotundifolia. She has also shown (Bielawska 1968) that C.gelida (referred to as C.scheuchzeri in her paper), a member of the Lanceolatae, can freely exchange genes with C.rotundifolia.

However, by all accounts, and judging from specimens examined, virtually all species of series other than the Vulgares can be easily distinguished from C.rotundifolia. This cannot be said of species in the series Vulgares itself, and indeed many of the species are distinguished largely on geographical grounds (table 3.5), specimens from Greenland are referred to C.gieseckiana and those from North America to C.intercedens by many authors (Böcher 1960, 1966). In these cases relatively little importance seems to have been given to whether these two species can always be distinguished from one another and from C.rotundifolia on morphological grounds alone. Shetler (1963) in his account of North American Campanulas in fact refers all his material to the one variable species C.rotundifolia. Kovanda (1970c), in his account for Flora Europea, submerges C.polymorpha in C.rotundifolia. All species of the series Vulgares would therefore seem to warrant careful study to elucidate their relationship with C.rotundifolia.

SECTION 5 - TAXA DESCRIBED FROM THE BRITISH ISLES

Apart from C.rotundifolia, C.gieseckiana (table 3.5 fig.3.2) is the only other species of the Heterophylla that has been identified in British material. There are two published records - Ben Nevis, Inverness-shire (Hruby 1930 as C.arctica); and limestone cliffs, Little Ormes Head, Llandudno, Caernarvonshire (Podlech 1965 p.116 as C.groenlandica). Also, several British specimens in the herbarium of the Edinburgh Botanic Gardens have been named C.groenlandica (= C.gieseckiana ssp.groenlandica) by Podlech (dated 1964). The localities are rather scattered : Lake District; Darlington, Yorkshire; Arran; Killin, Perthshire; Edinburgh; East Lothian; Fife; and Forfar. I admit to being unable to find any very obvious differences between these specimens and those he has labelled C.rotundifolia,

TABLE 3.5. DIFFERENTIAL CHARACTERS OF SPECIES OF THE SERIES VULGARES CLOSEST TO C.ROTUNDIFOLIA

F - Fedorov 1957; P - Podlech 1965, 1970; K - Kovanda 1970c; G - Gadella 1964; B - Bielawska 1968; Bö - Böcher 1966; H - Hulten 1968.

Character	C.rotundifolia	C.gieseckiana	C.intercedens	C.latisepala	C.langsdorffiana	C.polymorpha	C.asturica	C.wiedmannii
Habit	Prostrate-erect (G)	-	-	Lax, Decumbent (H)	-	-	-	-
Branching	Very variable	-	Little except towards top of stem (Bö)	-	-	-	Strongly patent (P)	Strongly patent (P)
Upper stem leaves	Linear, sessile (K) (F)	Petiolate(K) Spathulate(F)	-	Ovate to broadly lanceolate(H)	Linear (F)	-	-	-
Stem leaf tips	Usually acute (K)(P)(F)	Usually blunt (K)(P)(F)	-	-	-	Usually blunt(F)	-	-
Pubescence	Mostly pubescent(K)(P)(B) Mostly glabrous(F)	Mostly pubescent (K) Glabrous(F)	-	-	Glabrous (F)	Usually glabrous (B)(F)	Glabrous (P)	Glabrous(P)
Number of flowers per stem	(1-)few-many (K)(F)(P)(Bö)	1-few (K)(F) (P)(Bo)	Concentrated on upper part of stem few-many(Bö)	-	1-few (F)	Few (K)(P)(F)(B)	-	-
Ovary	Longer than broad (K)(P)	Broader than long. Hemispherical(K) (P)(Bö)	-	-	-	Large (B)	-	-
Calyx teeth	Short. Half corolla length or less (F)	Reddish-black appressed - slightly spreading	-	-	Long. Half corolla length or more(F) Ribbed. spreading (F)	Usually appressed(F)	-	-
Corolla size in mm	(10-)12-20(-30) (K)	(12-)14-25 (-30) (K)	-	Up to 30 (H)	-	Large (B) Up to 17 (F)	14 - 16	17 - 25
Pollen	Sometimes pale grey(Bö)	White	-	-	-	-	Pale Yellow(P)	Pale lilac (P)
Capsule stance	Nodding(K)(P)	Nodding(K)(P)	-	-	-	Nodding	More or less erect (P)	Nodding (P)

(a) C.latisepala(6x) (b) C.gieseckiana(2x) (c) as b. late season stems

fig. 3.2

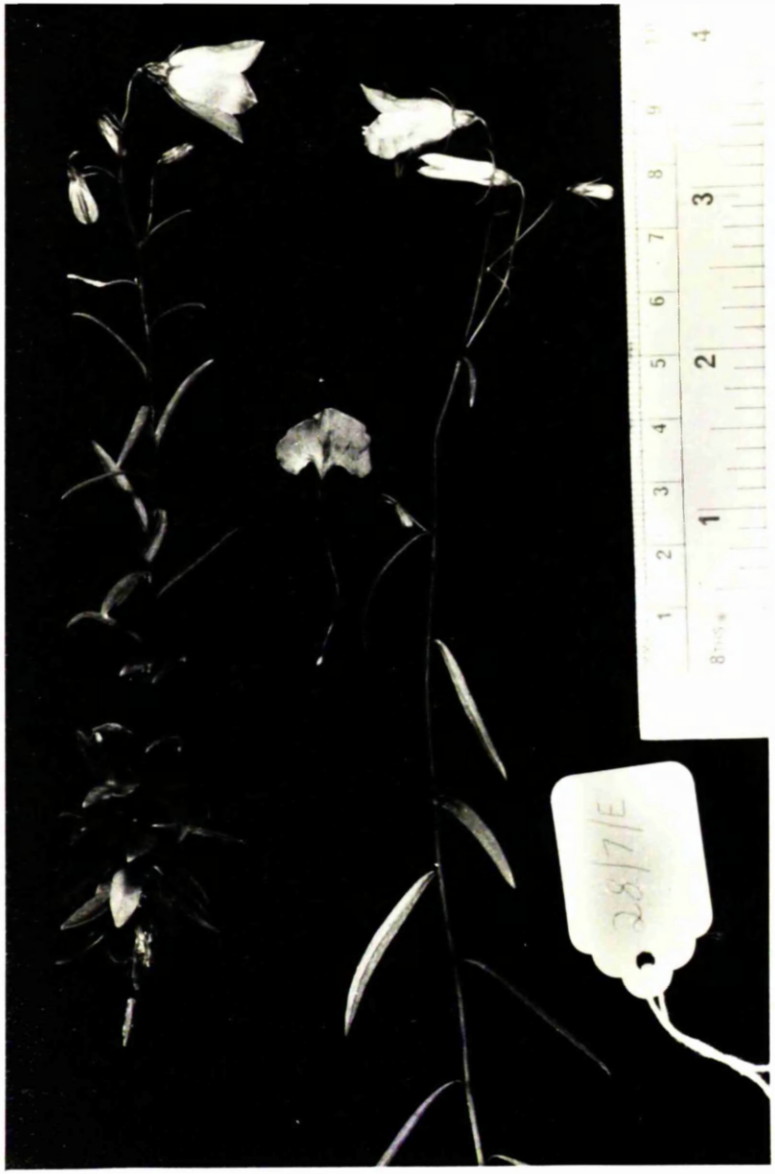


fig 3.3 C.ficarioides

though they do have large shallow flowers and hemispherical ovaries (i.e. the usual key characters of C.gieseckiana ssp.groenlandica). Otherwise they seem to be well within the variation range of Northern populations of C.rotundifolia. Hruby's work (1930) has been criticised by Kovanda (1970a)and Podlech (1965). However, herbarium specimens of C.gieseckiana from Greenland were little different from many northern and high altitude specimens from the British Isles.

Leaving aside consideration of C.gieseckiana, all herbarium specimens of native British material agreed more closely with C.rotundifolia s.s. than other continental species of the complex - with the possible exception of C.polymorpha, a species of dubious validity (see Kovanda 1970c and Chapter 10). From henceforth in this thesis British plants of this complex will therefore be referred to as C.rotundifolia.

SECTION 6 - THE SPECIES STUDIED IN THIS THESIS

In addition to material which could be referred to species of the series Vulgares (table 3.5), and which are morphologically very similar to C.rotundifolia, some material of other species was also studied. The characters distinguishing these species from C.rotundifolia and one another are shown in table 3.6 and discussed below.

C.cochleariifolia (2n = 34) fig 3.1. This is a diploid species of the series Alpicolae which typically looks very different from C.rotundifolia and is characteristically much shorter. The basal rosettes, in the axils of whose leaves the flowering stems are produced, are conspicuous, and persist throughout the flowering season. The basal leaves are bright green, glabrous, and dentate, and the petiole margins are ciliate. The flower buds are nodding and the flowers are small (less than 10 mm) and typically of a light blue colour.

TABLE.3.6 DIFFERENTIAL CHARACTERS OF SPECIES OUT WITH THE SERIES VULGARES DEALT WITH IN THIS THESIS

(After Kovanda 1970c, Quezel 1954, Willkomm and Lange 1861-1880).

Character	C.rotundifolia fig 1.1	C.scheuchzeri fig 3.1	C.ficarioides fig 3.3	C.cochleariifolia fig 3.1	C.mairei fig 3.4	C.arvatica fig 3.1
Roots	Thin	Thin	With napiform tubercles	Thin	Thin	Thin
Pubescence	Usually pubescent	Ciliate or glabrous	Ciliate or - glabrous	Ciliate, especially on leaf bases	-	-
Basal and Cauline Leaves	Heterophyllous	Heterophyllous	Heterophyllous	Heterophyllous	Heterophyllous	Isophyllous (Bracts narrower)
Basal Leaves at Anthesis	Usually absent	Absent	Absent	Present	-	Present
Flower Buds	Erect	Nodding	Nodding	Nodding	-	-
Corolla	Campanulate	Campanulate	Campanulate	Campanulate	?	Stellate

C.scheuchzeri (2n = 68, 102) fig 3.1. This species is rather more similar to C.rotundifolia, being taller growing with less persistent rosettes. The major distinguishing characters are the nutant flower buds and ciliate petioles, but the relatively short stems bearing few deep violet coloured flowers and the dark foliage give this species a distinctive appearance.

C.ficarioides (2n = 102) fig 3.3. This species is very similar in most respects to C.scheuchzeri, and differs primarily in possessing roots with carrot-like thickening.

C.mairei (2n = 16, 34) fig 3.4. Although not previously included in the Heterophylla, C.mairei is strongly heterophyllous. Unlike all species usually placed in the Heterophylla it is stoloniferous and has capsules opening by apical valves.

C.arvatica (2n = 28) fig 3.1. This species is not heterophyllous and does not belong to the subsection Heterophylla. Also, the flowers are open and star-shaped, not bell-shaped as in most of the Heterophylla. However, the basal leaves are very similar to those of C.asturica, with which is grows, and Crook (1951) mentions a hybrid between C.arvatica and C.rotundifolia. It was therefore considered that C.arvatica was worthy of study in relation to C.rotundifolia.

The number of topodemes examined morphologically and cytologically of each of the taxa discussed above are given in table 3.7

SECTION 7 - NOMENCLATURE

Table 3.8 is a list of all the species of Campanula mentioned in this thesis.

FIG. 3.4 Campanula mairei. Herbarium specimens collected in the wild in Morocco at 2,100m (7000ft) on Toubkal. Note the rotund leaves borne towards the base of the stem with more linear leaves above. The flowers and ripe capsules are erect.

TABLE 3.7

THE NUMBER OF TOPODEMES OF EACH SPECIES EXAMINED

C. rotundifolia	British	199
	European Non-British	9
C. asturica		6
C. gieseckiana	Iceland	7
C. gieseckiana	Greenland	1
C. intercedens		2
C. latisepala		1
C. cochlearifolia		1
C. scheuchzeri		1
C. ficarioides		1
C. mairei		1
C. arvatica		1

TABLE 3.8

A LIST OF ALL THE CAMPANULA SPECIES MENTIONED

IN THIS THESIS WITH AUTHORITIES

C.adsurgens Ler. et. Lev.
C.albanica Witas.
C.apennina Podl.
C.arctica (Lange) Hruby
C.arvatica Lag.
C.asturica Podl.
C.balcanica (Adam) Hruby
C.baumgartenii J.Becker
C.beckiana Hayek
C.bertolae Colla
ssp. bertolae
ssp.xylorrhiza (O.Schwarz) Podl.
C.bohemica Hruby
C.breynina Beck
C.bulgarica Witas.
C.caespitosa Scop.
C.cantabrica Feer.
C.carnica Schiede
C.cochleariifolia Lam.
C.corcontica Šourek
C.crassipes Heuffel
C.dubia A.DC.
C.excisa Schleicher
C.ficarioides Timb.- Lagr.
C.forsythii (Arcang.) Podl.
C.fragilis Cyr.
C.fritschii Witas.
C.garganica Ten.
C.gelida Kovanda
C.gentilis Kovanda
C.gieseckiana Vest
ssp.gieseckiana
ssp.groenlandica (Berl.) Böcher
C.groenlandica Berlin
C.gracillima Podl.
C.hercegovina Deg. et Fiala
C.herminii Hoffg. et Link
C.heterodoxa Vest
C.hispanica Willk.
C.intercedens Witas.
C.isophylla Mor.
C.jaubertiana Timb.- Lagr.
C.jurjurensis (Chab.) Witas.
C.justiniana Witas.
C.langsdorffiana Fisch.
C.latiseala Hulten
C.longisepala Podl.

TABLE 3.8 continued...

C.macrorrhiza J.Gay
C.marchesettii Witas.
C.mairei Pau
C.moravica (Spitz.) Kovanda
C.morettiana Rchb.
C.parryi A.Gray
C.pollinensis Podl.
C.polymorpha Witas.
C.praesignis G.Beck
C.precatoria Timb.- Lagr.
C.pseudostenocodon Lac.
C.pulla L.
C.recta Dulac
C.rhomboidalis L.
C.romanica Săvul.
C.rotundifolia L.
C.ruscinonensis Timb.- Lagr.
C.sabatia de Not.
S.scheuchzeri Vill.
C.serrata (Kit.) Hendrych
C.stenocodon Boiss.et Reut.
C.tanfanii Podl.
C.tommasiniana Reut.
C.trachelium L.
C.uniflora Vill.
C.velebitica Borb.
C.waldsteiniana R.& S.
C.wiedmannii Podl.
C.wilkommii Witas.
C.witasekiana Vlehr.
C.xylocarpa Kovanda

CHAPTER 4: CYTOLOGY

SECTION 1 - INTRODUCTION

In this chapter I shall discuss the cytological results obtained in the course of this study. Previous workers (Gadella 1964, Böcher 1960, Laane 1968, Morisset pers.comm, Löve and Löve 1965, Kovanda 1966a, 1966b, 1970a) have found all three cytodemes in Europe, the British Isles, and North America, though only diploids and tetraploids have been described from Greenland and Scandinavia. In several cases (Böcher 1960, Gadella 1964, Kovanda 1970a) small accessory (B) chromosomes have been reported from both diploids and tetraploids.

The cytology is being discussed before other aspects are dealt with as it presents the framework against which all other aspects of the variation must be viewed.

SECTION 2 - METHODS

Plants taken into cultivation were usually left undisturbed for about a month before any attempt was made to obtain root-tips from them for cytology. By that time there were usually rapidly growing roots lying between the soil and the sides of the pot. After the ball of soil had been removed from the up ended pot by sharp tapping, root-tips were easily removed with forceps without disturbing the soil. There is no evidence of any periodicity in the time of mitosis during the day as root-tips taken at all times from 9 a.m. to 9 p.m. yielded good mitotic figures.

Pretreatment

Root-tips were pretreated with a saturated aqueous solution of 1-bromo-naphthalene. It is only very slightly soluble in water, most of the reagent remaining at the bottom of the bottle. For use, the solution was decanted into vials to which the root-tips were added. A few globules of the reagent which float on the surface in the stock bottle are inevitably

carried over into the vials, but experience has shown that these have no detrimental effect.

The pretreatment time usually recommended with 1-bromo-naphthalene is two to four hours at room temperature. In practice I found it necessary to pretreat for four hours to obtain maximum contraction of the chromosomes. Shorter pretreatment times resulted in chromosomes which were too elongated and tended to be too intertwined and difficult to count. Increasing the pretreatment time to seven hours had very little effect on the quality of the final preparation.

After pretreatment, with whatever reagent, most published schedules usually insist on thorough washing. However, using the pretreatment method described above on root-tips of Campanula and several other genera (Dryopteris spp, Polypodium spp., Festuca ovina, Deschampsia spp:,) no deleterious effects could be detected if washing were omitted. This applied even if there were globules of 1-bromo-naphthalene around the root tips after the supernatant had been poured off. Omission of washing reduced the work involved in preparing the root tips, and by reducing the amount of handling necessary, cut losses and damage to the root-tips.

Fixation

After four hours pretreatment, the 1-bromo-naphthalene solution was decanted and about 10ml. freshly prepared 1:3 glacial acetic acid: 95% ethanol added to each vial.

Immediately after the fixative had been added the vials were transferred to the ice-box of a refrigerator, or a deep freeze, as low temperatures reduce the rate of formation of ethyl acetate. Leaving the root-tips in the fixative for twelve hours at room temperature, even if they were eventually placed in a deep freeze, greatly reduced the quality of the final preparations (the chromosomes were indistinct and there were many granules in the cytoplasm).

The longer the root-tips were stored in the deep freeze (at least up to six months) the better the final preparations, fewer granules being present in the cytoplasm. The use of either chloroform in the fixative or ether in the hydrolysing solution did not seem to rid the cytoplasm of granules as effectively as a long fixation period.

Normally the root-tips were left in the deep freeze until required for counting, although, if for any reason they could not remain there, after a minimum of 24 hours in the fixative they could be transferred to 70% ethanol and stored at room temperature. It was considered that the root-tips had to remain in the fixative for a minimum of 24 hours before they were hydrolysed.

Hydrolysis

Hydrolysis is required to enable the cells to be separated by tapping and squashing. The root tips were removed from the fixative, transferred to normal hydrochloric acid at 60°C and hydrolysed for 5 minutes in an oven or water bath. Hydrolysis for a shorter period than five minutes nearly always resulted (unless the root was very fine) in inadequate separation of the cells on tapping. Increasing the hydrolysis-time to up to 10 minutes gave satisfactory results, the cells being easier to separate and squash, but perhaps more susceptible to rupture. No damage to the chromosomes was noticed after longer hydrolysis.

After hydrolysis the root-tips were transferred to a few mls. of 70% ethanol in another vial. In this condition they have been stored successfully at room temperature for up to four years.

Staining

Initially staining with Feulgen and Snow's Carmine (Snow 1963) were tried, but these gave less satisfactory results than Dyer's (1963) Lacto-propionic orcein method. This stain was prepared by shaking up two grams

of orcein with 100 mls. of a mixture of 50ml acid and 50 mls. lactic acid, and filtering through a Whatman's No.1 filter paper. This stain was used directly, not after dilution as recommended by Dyer. In this undiluted state the lacto-propionic-orcein is extremely convenient to use, as temporary unringed preparations may be kept for up to six months without serious deterioration.

A disadvantage of this stain is that after about six months a fine precipitate forms in the stock bottle and must be removed by filtration. Some of the precipitate particles are about the same size as Campanula chromosomes though optically more dense. Great care was taken to remove the precipitate as its presence could lead to miscounting, especially if B-chromosomes were present in the material.

Preparation of slides and microscopy

A single root-tip was placed in a drop of 70% ethanol on a slide and examined with a dissecting microscope. In a root which had been growing actively, a dense area, which contained the highest proportion of dividing cells, was evident just behind the root cap. This extreme portion of the root-tip was carefully removed with dissecting needles and transferred to a drop of lactopropionic orcein stain. The root-tips were sufficiently fine so that no maceration with the needles was required. A coverslip was placed on the drop of stain containing the root-tip and tapped to separate the cells. The tapping was performed on the stage of the dissecting microscope so that the degree of dispersion of the cells could be controlled. The preparation was then placed between two layers of "Kleenex" tissue on an absolutely flat surface and squashed by pressure from the thumb. It was then scanned using a Zeiss photomicroscope. The positions of well-squashed cells were noted, and the chromosomes counted using a 100 x oil immersion phase contrast objective. Anisole (methyl phenyl ether) was

used in place of immersion oil as it is less viscous, and may be removed from both lens and coverslip by blotting with lens tissue without disturbing the specimen.

SECTION 3 - RESULTS

The chromosome numbers found in natural topodemes of C.rotundifolia in the British Isles, outside the British Isles, and in hybrids produced in cultivation are given in table 4.1 and in detail in table 4.2. A large number of accurate counts of 2n = 34, 68, 85, 88 and 102 were made from material collected in the wild and taken into cultivation. About half the total number of topodemes counted were represented by at least one plant in which the chromosome number was accurately determined. Particularly noteworthy is the record of two pentaploids (2n = 85) from the wild, no other pentaploids ever having been reported in nature, though they have been produced artificially in cultivation (Böcher 1966, Gadella 1964). Also most interesting is the count of 2n = 88 + 2B, presumably the result of a pentaploid×back-crossing to a hexaploid. The only previous record of an aneuploid count in wild collected material of the C.rotundifolia complex is that of 2n = 72 + 4B (Bocher 1963). Bielawska (1964), however, reports the production of aneuploids in cultivation with chromosome numbers approaching that of tetraploids (2n = 68).

B-chromosomes (Battaglia 1964) have previously been reported in the diploid (Gadella 1964, Kovanda 1970a) and tetraploid (Böcher 1960, Gadella l.c., Kovanda 1970a) cytodemes of C.rotundifolia. Up to three have been recorded in diploids, and up to four in tetraploids. In many of the published records a range of numbers is given for an individual plant, so it is clear that the numbers present in the cells of different roots, and perhaps even of the one root, may vary.

Because of their small size, and the large numbers of A-chromosomes, the exact number of B-chromosomes present in a cell is often difficult to determine, but in no case have I found the number to vary between different cells of the one plant. In my own studies no B-chromosomes were found in any of the diploids examined, but up to five were counted in tetraploids, and up to six in hexaploids. This is the first record of B-chromosomes in hexaploids of the C.rotundifolia complex, and is perhaps rather unexpected as B-chromosomes are often said to be infrequent at high polyploid levels.

Representative cells showing the tetraploid and hexaploid chromosome complements are shown in figs. 4.1, 4.2, and 4.3. As can be seen from these figures the chromosomes are small and very uniform in size. Karyological studies would therefore be impractical, though some differences between chromosomes might be obtained by fluorescence microscopy. Satellites are visible on some of the chromosomes (fig. 4.2).

As will be shown later (Chapter 5) it proved impossible to distinguish reliably between tetraploids and hexaploids on morphological grounds. To increase the number of points on the distribution map, a further set of cytological studies was undertaken in which a number of plants were examined cytologically and assigned to a polyploid level. For this purpose counts of 2n = 66-68 or 2n = 97-102 were accepted as tetraploid and hexaploid counts respectively. Only if obvious B-chromosomes were present were plants checked further. Any counts above the expected 68 or 102, were checked very carefully, as it is much less likely to overcount than to undercount, undercounting usually being due to one chromosome lying above another.

Although the above method involves making approximations, I consider it valid, as no accurately made count deviated even slightly from the expected. It seemed more important to classify a large number of plants

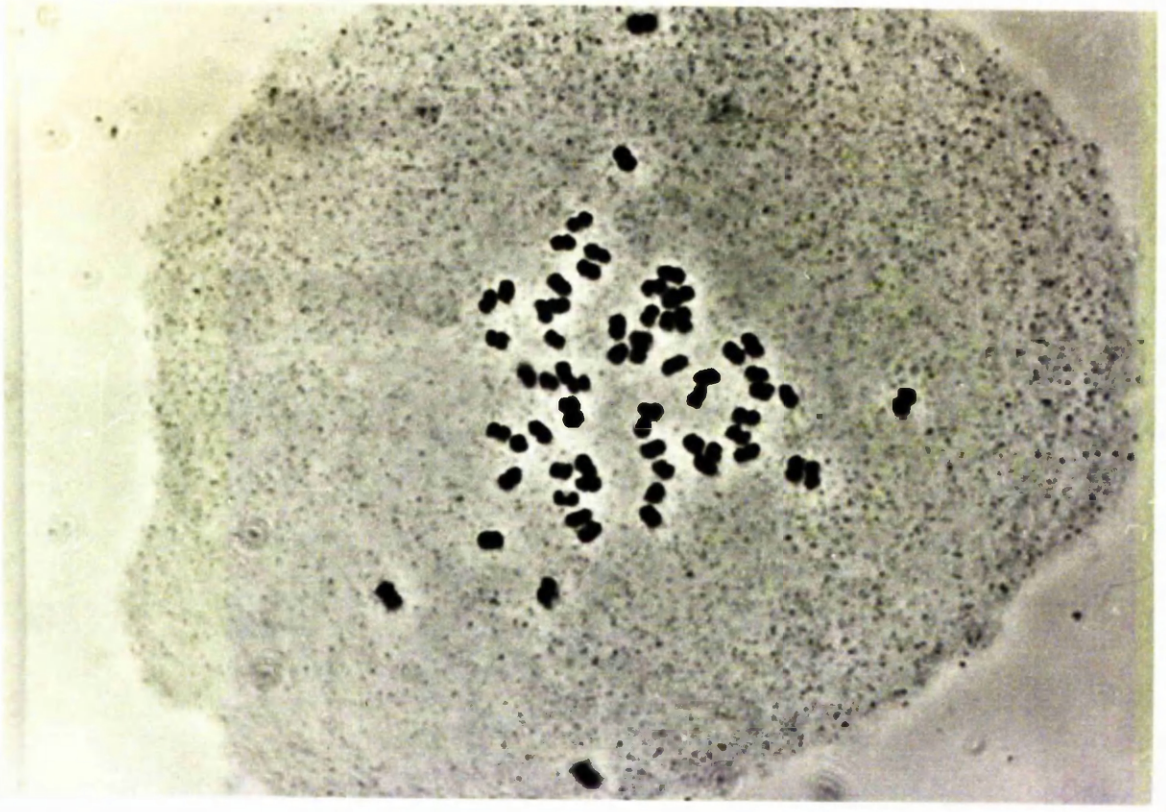
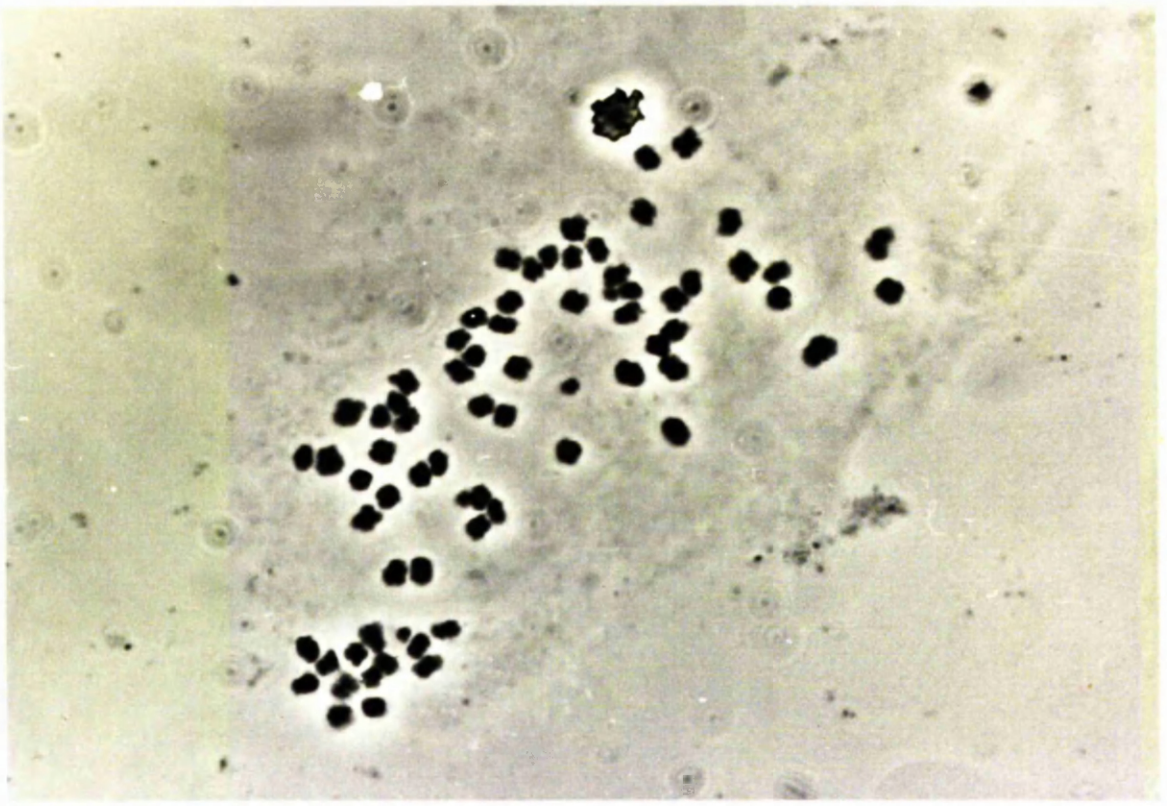


FIG. 4.1 Tetraploid cell (2n=68) of plant 3.8.B from Argyll.



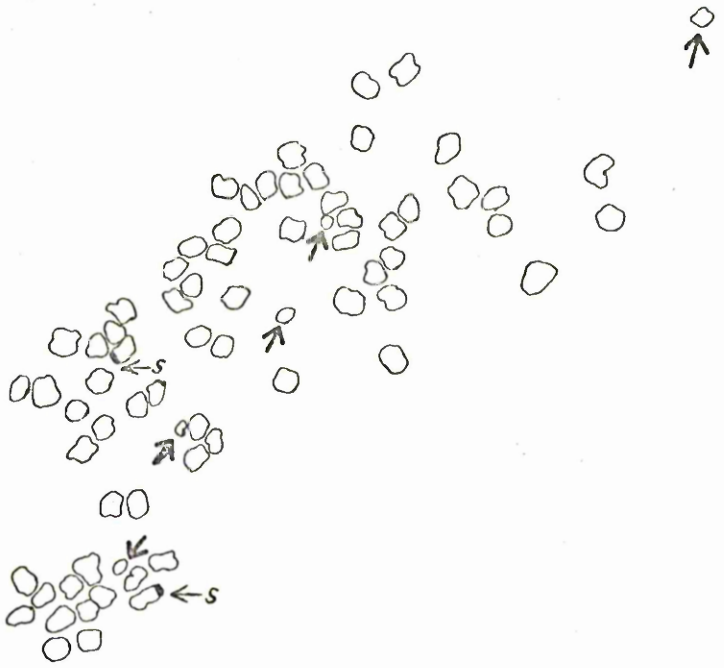
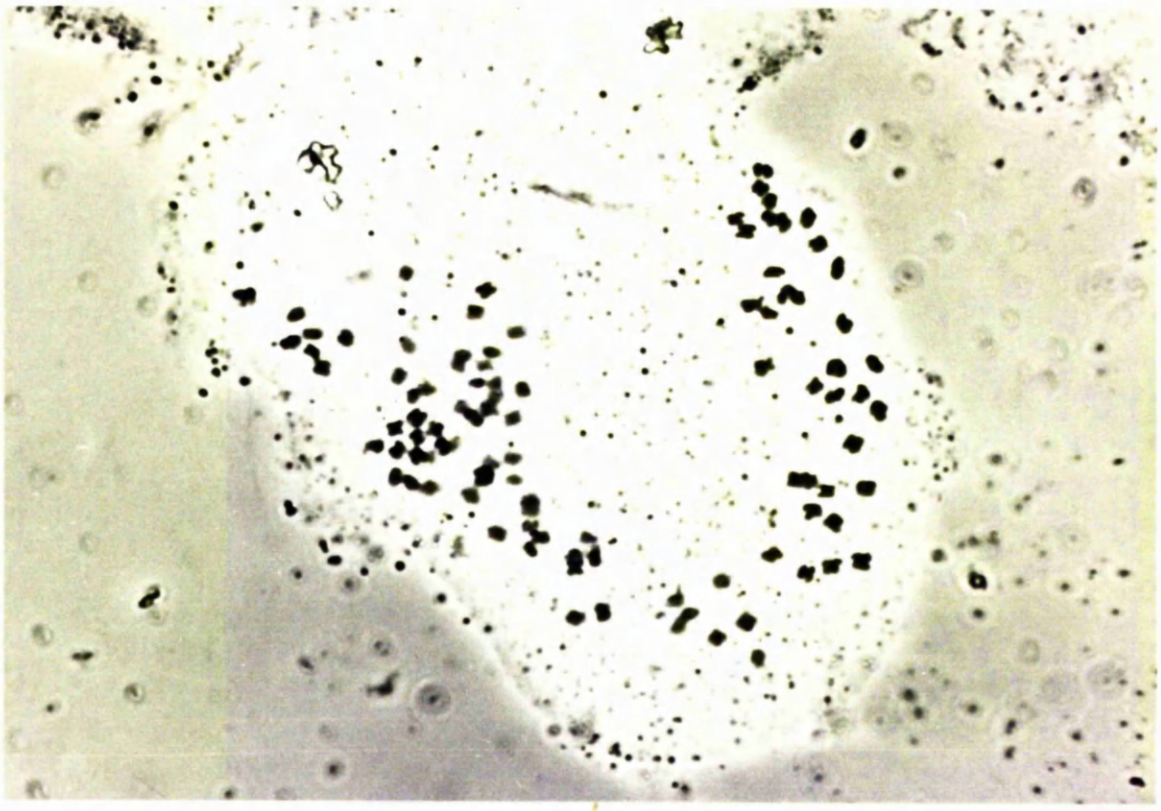


FIG. 4.2 Tetraploid cell (2n=68+5B) of plant 30.70.B from north Spain showing 5 B chromosomes (arrowed) and 2 chromosomes with satellites (denoted by S).



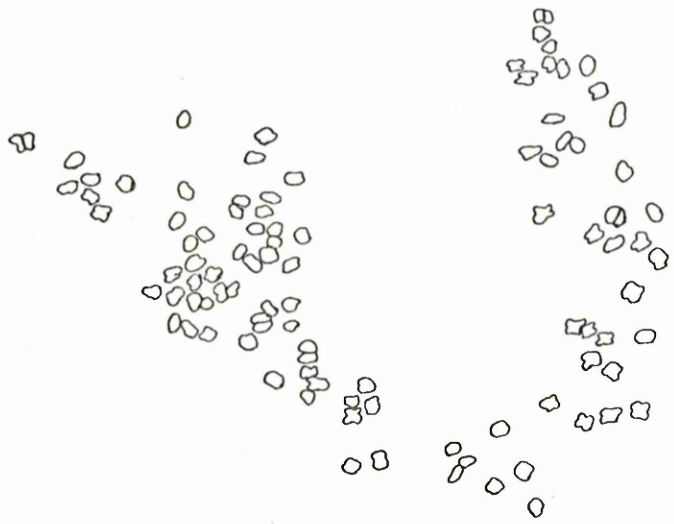


FIG. 4.3 Hexaploid cell (2n=102) of plant 10.7.A from Colonsay, Argyll.

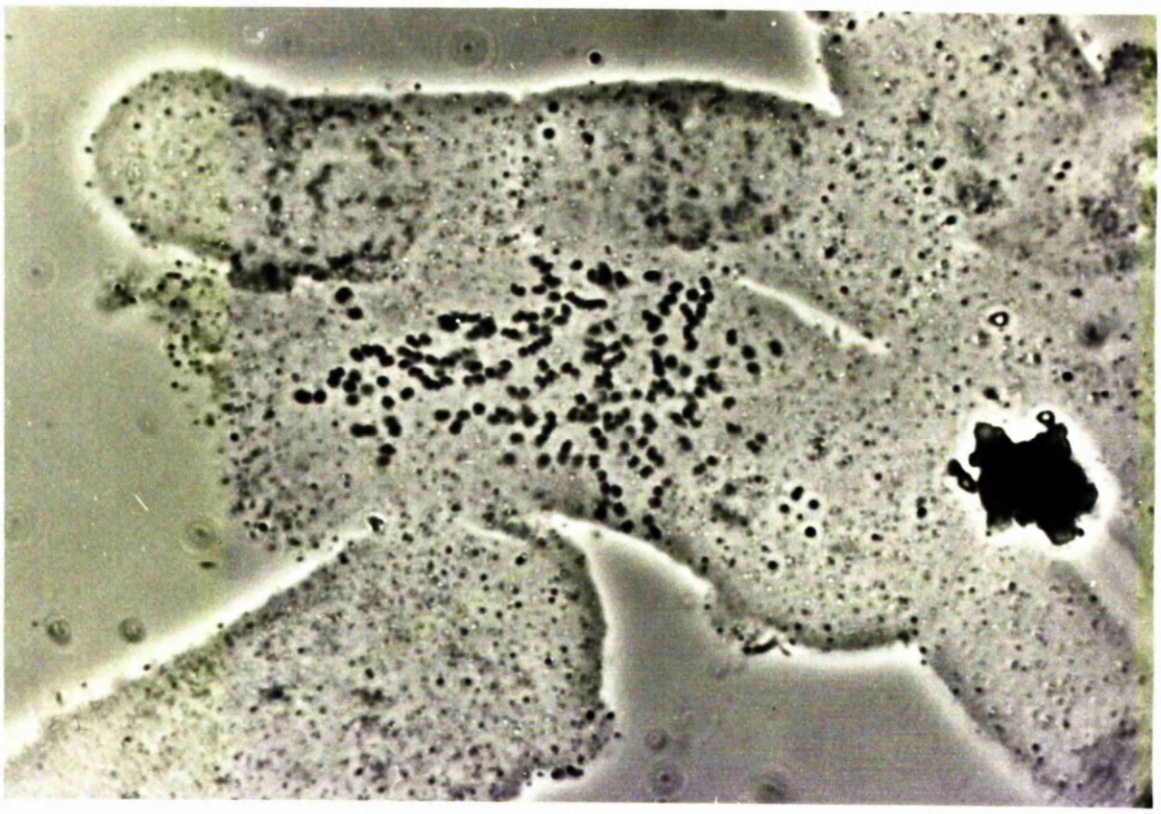


FIG. 4.4 Duodecaploid cell (2n=204) from otherwise hexaploid plant.

TABLE 4.1 SUMMARY OF CHROMOSOME NUMBERS FOUND IN NATURAL TOPODEMES AND EXPERIMENTAL HYBRIDS IN C.ROTUNDIFOLIA s.l.

The numbers in brackets are the number of topodemes examined.

	CHROMOSOME NUMBERS						
	DIPLOID	TRIPLOID	TETRAPLOID	PTEROPHYTE TRIPLOID	PENTAPLOID	HEXAPLOID	HEXAPLOID
NATURAL POPULATIONS							
British Isles	-	-	68(105)	-	85(2)	88(1)	102(63)
Continental Europe	34(2)	-	68(11)	-	-	-	102(1)
Greenland and Iceland	34(1)	-	68(7)	-	-	-	-
North America	-	-	68(2)	-	-	-	102(2)
ARTIFICIAL HYBRIDS	34	-	68	71-77	85	c90	102

TABLE 4.2 CHROMOSOME NUMBERS OF THE NATURAL TOPODEMES OF C.ROTUNDIFOLIA AND RELATED SPECIES INVESTIGATED

CHROMOSOME COUNTS

DIPLOIDS

Code No	2n	Locality	Habitat
		GERMANY (C.rotundifolia)	
48.B	34	Dessau, East Germany	Grass heath
67.8	34	Putzbrunn, Munich, West Germany	-
		GREENLAND (C.gieseckiana asp. gieseckiana)	
11.1	34	Midternaes, South West Greenland	-

TETRAPLOIDS

Code No	2n	Locality	Habitat	Grid Ref.
71.8	4x	Garbat, nr Garve, Ross and Cromarty	Streamside grassland	28/42-67-
59.8	4x	Findhorn, Moray	-	38/036647
70.8	4x	Tarvie, nr.Garve, Ross and Cromarty	Birch woodland	28/43-58-
80.8	4x	Connon Bridge, Ross and Cromarty	-	28/55-58-
81.8	68	Fort George, Inverness	-	28/781570
41.6	68+2B 68+4B	Muir of Ord, Ross and Cromarty	On dry stone wall	28/53-49-
43.6	4x	Drumossie, nr. Inverness	On dry stone wall	28/69-45-
69.8	4x	Auchnagall, nr. Moy, Inverness	Roadside grassland	28/76-36-
45.6, 68.8	4x	Insharn, nr.Carrbridge, Inverness	Roadside grassland	28/85-24-
46.6	4x	Aviemore, Inverness	Sandy embankment	28/89-11-
84.8	4x	Bridge of Don, Aberdeen	Sand dunes	38/95-11-
48.6	68	Newtonmore, Inverness	Grass heath	28/7--0--
50.8	4x	Dinnet, Aberdeenshire	Calluna heath	38/433000
39.6	4x	Dalwhinnie, Inverness	Grass heath	27/64-86-
8.0	68	Aonach Beag, Ben Alder Forest, Inverness	Sugar lime-stone grass land	27/455739

TABLE 4.2 (cont'd)

Code No	2n	Locality	Habitat	Grid Ref.
12.0	4x	Ben Alder, Inverness	Mountain grassland	27/495734
22.6, 23.6, 25.6	4x	Glendaruel, Argyll	Serpentine outcrop	26/0--8--
64.6	68	Carron Valley, Campsie Hills, Stirlingshire	Roadside grassland	26/65-86-
54.6	68	Campside Hills, Stirlingshire	-	26/7--8--
4.6,10.6	4x	Beinn Capuill, Tighnabruaich, Cowal, Argyll	Rock ledges	16/931795
11.6	4x	Lindsaig Farm, Kilfinan, Cowal, Argyll	Dry stone wall	16/931795
13.6	4x	Drum Farm, Kilfinan, Cowal, Argyll	Roadside grassland	16/929764
16.6	4x	Kilfinan, Cowal, Argyll	Copper mine	16/942792
20.9	68	Eas an Duin, Tighnabruaich, Argyll	Wooded gorge	16=978735
65.6	68+3B	Cramond Island, nr. Edinburgh	-	36/19-78-
13.0	68	Arthur's Seat, Edinburgh	Rock ledge	36/274725
1.8	4x	Sheeppath Dean, nr. Dunbar, E. Lothian	-	36/69-70-
66.6	68	Cockburnspath, Berwickshire	Grassy maritime cliffs	36/77-72-
15.6	68	Carry, Tighnabruaich, Cowal, Argyll	Machair	16/988672
2.7	68	Ardlamont Point, Cowal, Argyll	Machair	16/988641
3.7	68	Ardlamont Point, Cowal, Argyll	Maritime cliffs	16/988642
36.7	4x	Bigholm, Beith, Ayrshire	Rock ledges	36/3--5--
34.6,35.6	68	Pirnmill, Arran, Bute	-	16/8--4--
6.8	4x	Fenwick Moor, Renfrewshire	-	26=584486
44.9	68	Falls of Clyde, Lanark	River gorge	26/8--4--
7.7, 8.7, 9.7	4x	Cheswick, nr. Berwick-on-Tweed	Sand dunes	46/046477 46/036475 46/051461
14.8	4x	Dunure, Ayrshire	Maritime cliffs	26/253159
87.8	4x	Leadhills, Lanarkshire	-	26/885166
19.7	68+1B, 68	Palmullan Burn, Straiton, Ayrshire	Hill grass land	26/374013
53.6	4x	Nithsdale, nr Sanquhar, Dumfries	-	26/832062
51.6	68	Byne Hill, Girvan, Ayrshire	Serpentine grassland	25/18-95-
90.6	4x	Whitburn, Co. Durham	-	45/4--6--
72.6	68	Allonby, nr. Maryport, Cumberland	-	35/0--4--
44.8	68	Langdon Bank, Upper Teesdale	-	35/8--3--
4.0	4x	Ireshopeburn, Weardale, Co. Durham	Lead mine	35/859384

TABLE 4.2 (cont'd)

Code No	2n	Locality	Habitat	Grid Ref.
17.0	68	Little Fell, nr. Appleby, Westmorland	Limestone grassland	35/784224
45.8	4x	High Force, Upper Teesdale, Co. Durham	-	35/88-28-
5.0, 6.0	68	Thistle Green, Cronkley Fell, Upper Teesdale, Yorkshire	Sugar/limestone	35/843284
73.6	4x	Watendlath Fell, Borrowdale, Cumberland	-	35/2--1--
1.2	68	Striding Edge, Helvellyn, Westmorland	Mountain rock ledge	35/3--1--
49.6	4x	Chaoruinn, nr. Dalnaspidal, Inverness	Streamside flushes	27/65-76-
25.9	68	The Cairnwell, Devil's Elbow, Aberdeenshire	Mountain limestone	37/127780
36.6, 38.6	68	Struan, nr. Blair Athol, Perthshire	River gorge and grassland	27/81-65-
34.9, 35.9 43.9	68	Ben Lawers, Perthshire	Mountain ledges and grassland	27/645419 27/637415
59.6	4x	Parkhill, Arbroath, Angus	-	37/648454
42.7, 43.7, 44.7	68	Beinn Udlaidh, Glen Orchy, Argyll	Mountain ledges and Rhacomitrium heath	27/2--3--
77.7	68	Ben Dorain, Bridge of Orchy, Argyll	Mountain ledges	27/325378
18.9	4x	Lead mines, Tyndrum, Perthshire	Rock ledges	27/3--3--
50.6	68	Amulree, Perthshire	Grass heath	27/92-37-
88.6	68	Stob Garbh, Ben Lui, Perthshire	Mountain ledges	27/2--2--
80.7	4x	Waterfall on Eas Anie, Tyndrum, Perthshire	Rock ledges	27/289285
5.8	4x	Cononish, nr Tyndrum, Perthshire	Riverside	27/300285
63.6	68	Crianlarich, Perthshire	Grassland	27/3--2--
16.9	4x	Gruach Ardrain, Crainlarich, Perthshire	Mountain ledges	27/407212
28.9	68	Stob Binnein, nr Crainlarich, Perthshire	Mountain ledges	27/434226 27/440220
20.7	4x	Kirkton Glen, Balquhidder, Perthshire	-	27/52-24-
76.7	4x	Binnein An Fhidleir, nr. Inveraray, Argyll	Mountain ledges	27/230107
17.9	68	An Caisteal, Glen Falloch, Crianlarich, Perthshire	Mountain ledges (3000')	27/382188
7.8	4x	Beinn Chabhair, Glen Falloch Crianlarich, Perthshire	Mountain ledges (2750')	27/365180
29.6	4x	Glen Kinglass, nr. Inverary, Argyll	Molinia grassland	27/235096

TABLE 4.2 (cont'd)

Code No	2n	Locality	Habitat	Grid Ref.
89.6	4x	Ben Ime, nr.Arrochar, Argyll	Mountain ledges (2750')	27/254088
72.7	68	Ben Arthur, nr.Arrochar, Argyll	Mountain ledges	27/26-05-
4.6, 6.6	68	Ben an Lochain, nr.Arrochar, Argyll	Ledges and Rhacomitrium heath (1500-2900')	27/221075 27/217079
98.6	4x	Strathlachlan, nr.Strachur, Argyll	-	26/01-95-
17.6	4x	Creag Tharsuinn, nr.Dunoon, Argyll	Rock ledges	26/086903
18.6	68	Carrachra, Glen Massan, nr.Dunoon, Argyll	Rock ledges	26/091905
20.6	68	Beinn Mhor, nr.Dunoon, Argyll	Rock ledges	26/097907
94.6	4x	Rumbling Bridge, Kinross-shire	Grassland	36/019993
41.7	4x	Silverdale, nr.Carnforth, Lancs	Sand dunes	34/46-75-
76.6, 79.6	68	Strensall, Yorkshire	Grass heath	44/649615 44/640618
46.8	4x	Inglewhite, Lancashire	-	34/539403
68.6, 71.6	4x	Midhope Stocksbridge, Yorkshire	-	43/217997 43/230996
70.6	68	Buxton, Derbyshire	-	43/054718
89.8	4x	Tideswell, Derbyshire	-	43/1--7--
80.6	4x	Monksdale, Derbyshire	Limestone cliffs	43/1--7--
70.7	4x	Norfolk	-	53/827223
38.9, 27.9	68	Whin Common, Downham Market, Norfolk	Grassland	53/617010
69.6	4x	Castor Hanglands, nr. Peterborough, Huntingdon	-	52/1--9--
60.6	4x	Pont Erwyd, Cardinganshire	-	22/7--8--
31.6	68	Breckland, nr. Brandon, Suffolk	-	52/798829
64.8	4x	Thetford, Norfolk	Woodland	52/8--8--
81.6	4x	Beccles, Suffolk	-	62/3--8-- 62/4--8--
65.8	4x	Dunwich, Suffolk	-	62/3--7-- 62/453722
86.6	4x	Cavenham Heath, Suffolk	-	52/7--6--
66.8	4x	Dunwich, Forest, Suffolk	-	62/4--6--
1.7, 65.7	68	Fleam Dyke, Cambridge	Chalk grassland	52/55-55-
64.7	68	Dunstable Downs, Bedfordshire	-	52/00-21-
55.8	4x	Farleigh, Warlingham, Surrey	-	51/36-61-
60.7	4x	Isle of Wight	-	40/4--8--
		NORWAY		
4.7	4x	Norway	Woodland	-
		HOLLAND		
56.8	4x	Wageningen	-	-

TABLE 4.2 (cont'd)

Code No	2n	Locality	Habitat	Grid Ref.
		GERMANY		
52.8	4x	Black Forest	-	-
		AUSTRIA		
58.8	4x	Turnitz	-	-
60.8, 61.8	4x	Rotmoosferner	-	-
62.8	4x	Niedertai	-	-
		SPAIN		
24.7	68	Gorge of Rio Cares, nr.Panes, Oviedo	Limestone cliffs	-
25.7	68	Gorge of Rio Deva, La Hemida, nr. Potes, Oviedo	Limestone cliffs	-
22.7, 23.7	4x	Los Lagos, nr.Covadonga, Oviedo	On limestone	-
30.7	4x 68+58	Pena Santa, nr.Covadonga, Oviedo	Limestone rock crevices 2500m (8000')	-
26.7	4x	Djedo, nr.Potes, Oviedo	Limestone scree	-
		ICELAND		
9.1	68	Dyrafjördur, N.W. Peninsula	-	-
2.1	4x	Gilsbakki Farm, Hvitarsida, W. Iceland	Streamside in pasture	-
3.1	4x	Egilsstadir, E. Iceland	Stony grassland birch wood	-
4.1	4x	Fagridalur, E. Iceland	Stony grass heath	-
5.1	68	Helgusstadir, E.Iceland	Maritime pasture	-
6.1	4x	nr. Tunga Farm, Breidafjördur, E. Iceland	Mountain grassland	-
7.1	68	Breidalsheidi, E. Iceland	Fell field	-
		CANADA		
37.9	4x	Newfoundland	-	-
	4x	Lake Superior	Sand dunes	-

PENTAPLOIDS AND HYBRIDS

Code No	2n	Locality	Habitat	Grid Ref.
33.9.A	85	Ben Lawers, Perthshire	Mountain ledges	27/636408
34.9.A	85	Ben Lawers, Perthshire	Mountain ledges	27/637415
22.9.B	88+2B	Garvie Farm, Glendarvel, Argyll	Pasture	26/0--8--

TABLE 4.2 (cont'd) HEXAPLOIDS

Code No	2n	Locality	Habitat	Grid Ref.
76.8	6x	An Fharaid, Durness, Sutherland	Sand dunes	29/389705
72.8	6x	Sandwood Bay, nr. Durness, Sutherland	Sand dunes	29/226656 29/216648
73.8, 74.8	6x	Borralie, Durness, Sutherland	Limestone crevices	29/387653 29/385653
75.8	6x	Smoo cove, Durness, Sutherland	Limestone grassland	29/418672
42.8	6x	Dun Glas, Helmsdale, Sutherland	-	39/058173
37.7	6x	Helmsdale, Sutherland	-	29/95-09-
53.7	6x	Northton, South Harris, Inverness	Sand dunes	08/9--9--
57.7	102	Seilbost, South Harris, Inverness	Dune pasture	18/0--9--
77.8	6x	Inveran, Sutherland	Heathy road-side grass-land	28/57-97-
78.8	6x	Bonar Bridge, Sutherland	Roadside grassland	28/60-91-
82.8	6x	Tain, Ross and Cromarty	-	28/810837
79.8	6x	Evanton, Ross and Cromarty	Roadside grassland	28/6--7--
85.8	6x	South Uist, Inverness	-	08/72-23-
45.6	6x	Carrbridge, Inverness	Roadside grassland	28/84-24-
29.9	102	N.E.Coir, Aonach Beag, Nevis range, Inverness	Rock ledges	27/198720
30.9	102	Carn Mor Dearg, Nevis Range, Inverness	Rock ledges	27/175714
9.0	102	Ben Alder, Inverness	Rock ledge and Rhacomi-trium heath	27/487719
61.6, 62.6	102	Strontian, Inverness	-	17/8--6--
91.8	6x	Calgary, Mull	Machair	17/3--5--
25.8		Dervaig, Mull, Argyll	Roadside grassland	17/416518
24.8	6x	Ensay, Mull, Argyll	Grass heath	17/361497
23.8	6x	Dishig, on Loch na Keal, Mull, Argyll	Machair	17/492358
29.8, 30.8, 31.8	6x	Ben More, Mull, Argyll	Grassland Rock ledges Rhacomitrium heath	17/516340 17/528332 17/524333
22.8	6x	Carsaig, Mull, Argyll	Seaside rock ledges	17/52-20-
3.6, 55.6	6x	Ardbhaan Cliffs, Oban, Argyll	Seaside cliff	17/83-28-
1.6, 2.6,	6x 102+3B	Dun Mor, Easdale, Argyll	Maritime cliffs	17/7--1--
75.7, 1.1	102	Beinn an Lochain, nr. Arochar, Argyll	Mountain ledges	27/221075 27/219075
16.7	102+6B	Balnahard Bay, Colonsay, Argyll	Sand dunes	17/426003

TABLE 4.2 (cont'd)

Code No.	2n	Locality	Habitat	Grid Ref.
14.7	102+2B	Uragaig, Kiloran Bay, Colonsay, Argyll	Machair	16/391984
62.7	102	Lochain na Sgoltaire, Colonsay, Argyll	Rock ledges	16/389978
10.7	102	Scalasaig, Colonsay, Argyll	Roadside grassland	16/395940
11.7	6x	Rubh an Dorain, Scalasaig, Colonsay, Argyll	Limestone pavement	16/406950
11.8	6x	Inverlussa, nr. Tayvallich, Knapdale, Argyll	-	16/77-86-
21.6, 21.9, 22.9	6x	Garvie Farm, Glendaruel, Argyll	Wooded gorge	26/0--8--
21.8	6x	Ben an Oir, nr. Kilberry, Jura, Argyll	Calluna heath	16/497746
10.8	6x	Isle of Danna, nr. Tayvallich, Knapdale, Argyll	-	16/69-78-
18.7	102	Port Askaig, Islay, Argyll	Maritime cliffs	16/42-69-
39.8	6x	Tangy, Machrihanish, Kintyre, Argyll	-	16/655275
41.8	6x	Machrihanish, Kintyre, Argyll	-	16/655260
39.7	6x	Campbeltown, Kintyre, Argyll	-	16/744213
100.6	102	Wanlockhead, Lanarkshire	-	26/8--1--
86.8	6x	Southend, Kintyre, Argyll	Sand dunes	16/599072
13.8	102	Summit Plateau, Merrick Kircudbridghtshire	Rock ledges and Salix herbacea heath	25/428854
		ENGLAND		
24.9, 3.0	102	Widdybank Fell, Upper Teesdale, Co. Durham	Limestone grassland	35/815308
6.9	6x	Widdybank Fell, Upper Teesdale, Co. Durham	-	35/809295
1.0	102	Widdybank Fell, Upper Teesdale, Co. Durham	Limestone grassland	35/814295
2.0	102	High Force, Upper Teesdale, Co. Durham	Cliffs and riverside	35/883285
101.6	102	The Cronk, Isle of Man	Grassland and maritime cliffs	24/337960
74.7	6x	Upper Foxdale, Isle of Man	-	24/279775
59.7	6x	Kynance Cove, Lizard, Cornwall	Maritime rock ledges	10/686135
92.6	6x	Lizard, Cornwall	-	10/7--1--
		IRELAND		
69.7	6x	Ballintoy, Ballycastle, Co. Antrim	Coastal cliff ledges	16/2--0--
61.7	6x	Slieve League, Donegal	-	95/6--4--

TABLE 4.2 (cont'd)

Code No	2n	Locality	Habitat	Grid Ref.
63.7	102+4B	Whitehead, Belfast	-	15/6--4--
19.8	6x	Ben Bulbin, Sligo	Mountain rock ledges	95/7--1--
20.8	6x	Lough Cullin, nr.Pontoon, Co.Mayo	Rock crevices	94/3--8--
17.8	6x	Mannin Bay, nr.Clifden, Connemara, Co. Galway	Coral sand	84/6--2--
16.8	6x	Muckanaght, Twelve Bens, Connemara, Co. Galway	Rock ledges	84/7--2--
18.8	6x	Dog's Bay, nr Clifden, Connemara, Co. Galway	Shell sand	84/7--1--
31.7	102 102+2B	Black Head, Co. Clare	Limestone pavement	93/1--8--
71.7	6x	Mivinish, S. W. Galway	-	93/7--6--
88.8	6x	Lough Derg, Co. Tipperary	-	93/8--5--
93.6	6x	Galtee Mts., Co. Tipperary	-	92/7--9--
		SPAIN		
21.7	6x	Alevia, Nr. Panes, Nr. Potes, Oviedo	Genista hispanica-Erica vagans heath on limestone	-
		CANADA		
97.6	102	Isle Gaspé, Quebec	-	-
		ALASKA		
14.1	102	Alaska	-	-

OTHER SPECIES OF CAMPANULA INVESTIGATED

Code No	2n	Locality	Habitat
C.cochleariifolia			
63.8	34	Neudorf die Umhausen, Otztal, Austria	-
C.scheuchzeri			
61.8	4x	Rotmoosferner, Otztal, Austria	-
C.ficarioides			
28.7	68	Peurto de st. Glorio, nr. Panes, Oviedo, Spain	Shale gravel
C.mairei			
	34	Toubkal, Morocco	Beside irrigation ditch
C.arvatica			
	28	Los Lagos, nr Covadonga, Oviedo, Spain	Limestone rock ledges

as either tetraploids or hexaploids, rather than to know accurately the chromosome number of fewer plants. However, I admit this could mean that I might miss such discoveries as Böcher's (1963) find of a plant with 2n = 72 + 4B, near Termignon in the French Alps, though the difference between 2n = 72 + 4B and 2n = 68 + 8B could only be certainly detected by meiotic studies. At one stage two plants from Beauly in Inverness-shire did appear to have 2n = 70, but study of further mitotic preparations convinced me that two of the chromosomes were smaller than the rest, and the final count was recorded as 2n = 68 + 2B.

Cells containing 136 and 203 (presumably a mis-count for 204, but only 203 chromosomes could be seen) chromosomes were found in preparations containing otherwise only tetraploid and hexaploid cells respectively (fig.4.4).

SECTION 4 - MEIOSIS

Introduction

Böcher (1960) has carried out extensive studies on the meiosis of diploid and tetraploid plants of C.rotundifolia s.s and C.gieseckiana. Though some plants were largely bivalent forming, others sometimes formed large chromosome associations at meiosis. These associations were interpreted as resulting from translocation heterozygosis as has been described in Oenothera (Catcheside 1930) and Campanula persicifolia (Gairdner and Darlington 1931, Darlington and Gairdner 1937). In C.rotundifolia Böcher (1960) reports that the formation of large chromosome associations at meiosis may seriously reduce the fertility of a plant, presumably as a result of irregular segregation of the chromosomes at anaphase I. In some plants anaphase bridges were frequent. In a later paper Böcher (1964) attributed much of the association between chromosomes at meiosis in C.rotundifolia to "stickiness", which could be due to technical factors, but might also have a genetic component.

Bielawska (1968) in a study of Polish tetraploids records only bivalent formation.

Methods

The method employed was to fix buds 1-2 mm long in freshly prepared 1 to 3 acetic alcohol and, after at least 24 hours fixation, to dissect out a stamen and mount it in a drop of the lacto-propionic orcein stain. Using needles, the stamen was punctured and squeezed to expel the pollen mother cells, the remains of the stamen removed, and the preparation squashed in the same way as a root-tip preparation.

Results

Tetraploid (77-7-A and 1.1.B) and hexaploid (20.8.D and 1.1.A) plants were examined to see if there were any meiotic irregularities (bridges or laggards at anaphase I). No such irregularities were found. If the behaviour of these samples is typical of British material, it would seem that bivalents are produced at meiosis and synapsis is normal.

The fact that no marked reduction in fertility, as assessed by seed production following open pollination, was noticed in any of the 500 or so plants maintained in cultivation also argues against any major occurrence of meiotic irregularities.

SECTION 5 - CONCLUSIONS

Mitosis

Despite the very small chromosome size and the high chromosome numbers, many accurate mitotic counts have been made from root tip squashes. Tetraploids and hexaploids have been recorded from the British Isles, pentaploids have been recorded for the first time from the wild, and many aneuploids have been produced in cultivation. The presence of B-chromosomes in tetraploids has been confirmed, and B-chromosomes have been recorded for the first time in hexaploids.

Meiosis

After initial difficulties the techniques required for meiotic studies in C. rotundifolia have been mastered. Unfortunately only a few observations have yet been made, but in further work it is planned to study meiosis in representatives of many topodemes. Particular attention will also be paid to triploids, pentaploids and interspecific hybrids.

CHAPTER 5. MORPHOLOGY

INTRODUCTION

In the previous chapters evidence has been presented to demonstrate that more than one taxon of the C.rotundifolia group may occur in Britain and at least two cytodemes are present. It was obvious from casual observation of herbarium specimens, wild material, and plants in cultivation, that the variability was very great. It was therefore decided to make extensive observations on a very wide range of material rather than to restrict myself to detailed observations of a few genotypes as has been done in most previous studies (Böcher 1960, Gadella 1964, Bielawska 1968, Kovanda 1970a). In all, five to six hundred plants were observed in cultivation over from two to six years. In addition, a few genotypes representing both the averages and the extremes of variation were selected for detailed biometrical study.

Two particular objects were kept in mind in all morphological observations (a) could the cytodemes be separated on morphological grounds and therefore be described as separate taxa: (b) to what extent was the variation habitat correlated. Previous workers (Böcher 1960, Hubac 1961, Gadella 1964) have been unable to separate the three cytodemes of C.rotundifolia s.s.

In other related species in which two cytodemes have been discovered (e.g. C.gieseckiana, C.scheuchzeri), similar difficulties have been reported. Since the original work of Turesson (1925, 1930) no major work has been undertaken on the ecological differentiation within C.rotundifolia, although some authors do make comments on the morphology of plants from particular habitats (Böcher 1960, Bielawska 1968, Kovanda 1970c).

Throughout the course of this work, numerous characters have been subjectively assessed for their usefulness in separating the cytodemes, and finally pollen size, seed size, and testa cell width were selected for objective assessment as the characters most likely to give a taxonomic separation, and

which were amenable to statistical treatment.

The variation in individual characters will be discussed in order beginning with vegetative and finishing with floral characters. The headings to be used are:-

Plant size	Section	2
Rhizome development	"	3
Leaves	"	4
Hairiness	"	5
Hair size	"	6
Number of flowers per stem	"	7
Habit	"	8
Flower size and shape	"	9
Flower colour	"	10
Pollen colour	"	11
Ovary shape	"	12
Pollen diameter	"	13
Seed size	"	14
Seed weight	"	15
Criticism of data on seed characters	"	16
Testa cell lumen width	"	17

SECTION 2 - PLANT SIZE

It is sometimes stated that within groups of related taxa differing in polyploid level, those at the higher polyploid levels are usually larger and thicker in all their parts. Although this may be true of some artificially created polyploids, it is not generally the case, especially with natural polyploids (Lewis and John 1963, ~~Bowden 1940~~).

However, even if such size differences were visible in cultivation under constant conditions, phenotypic variation due to environmental differences would probably make most size characters useless taxonomically with herbarium specimens. This focused attention on the usually more constant floral characters.

In cultivation in pots the tetraploid cytodeme yielded both the tallest and the shortest plants (fig. 5.1). The hexaploids did seem on the whole to have thicker stems, but this was more closely correlated with ovary and corolla size, (which were generally greater in hexaploids) and position of the flower on the stem, than with polyploid level itself.

FIG. 5.1 Tallest and shortest British plants - both tetraploid. Left - 86.6.C from Cavenham heath, Norfolk. Right - 41.6.B from Muir of Ord, Ross and Cromorty.

FIG. 5.2 Hexaploid from Muckanaght, Connemara, Co. Galway (16.8.A).

SECTION 3 - RHIZOME DEVELOPMENT

Although C.rotundifolia is said to have slender creeping rhizomes (Clapham et al. 1962, Kovanda 1970c), individuals have been found in which rhizome development is greatly reduced. As described in Chapter 7, rhizomes first arise from the upper regions of the tap root of a seedling, or from the axils of the primary rosette leaves, and further rhizome development is from the axils of the scale leaves on such rhizomes. The rhizomes are initially usually positively geotropic to plagiotropic, growing somewhat downwards into the soil, and in pots sometimes emerging through drainage holes in the bottom in a tuft of green leaves. Later they usually become plagiotropic to negatively geotropic, rising towards the surface to produce either a rosette of basal leaves or a flowering shoot. Leaf development seems to be controlled by light, a rhizome in darkness deep in the soil or in a crevice will produce only scale leaves, while one near the surface (though still growing horizontally) or appressed to the inside of a somewhat translucent pot (plastic pots are rarely completely opaque) will develop normal basal leaves on long petioles. Since the growth habit of the rhizomes is plagiotropic, there is a suggestion that C.rotundifolia growing on vertical and near vertical cliffs might spread laterally more rapidly than it would spread vertically, and observations suggest that this is so.

The length to which a rhizome will grow before emerging to form a rosette is probably to a large extent controlled by the vigour of the plant, but a certain component of the variation is genetic as some individuals regularly produce many long (up to 0.5m) rhizomes, while others only produce short rhizomes. Plants from grassland always have long rhizomes, while cliff plants may have long and short rhizomes.

The plant with the shortest rhizomes (if they could be called such) (no. 16/8/A, fig. 5.2) was a hexaploid from a cliff ledge on Muckanaught, Connemara,

FIG. 5.3 The exposed maritime cliffs of Dun Mor at Easdale south of Oban.

FIG.5.4 Cultivated specimens of plants from Easdale (1.6). The largest specimen was grown normally while the others were droughted and have protruding stigmas and (extreme ~~left~~ right) 9n 4 abnormally dissected flower.

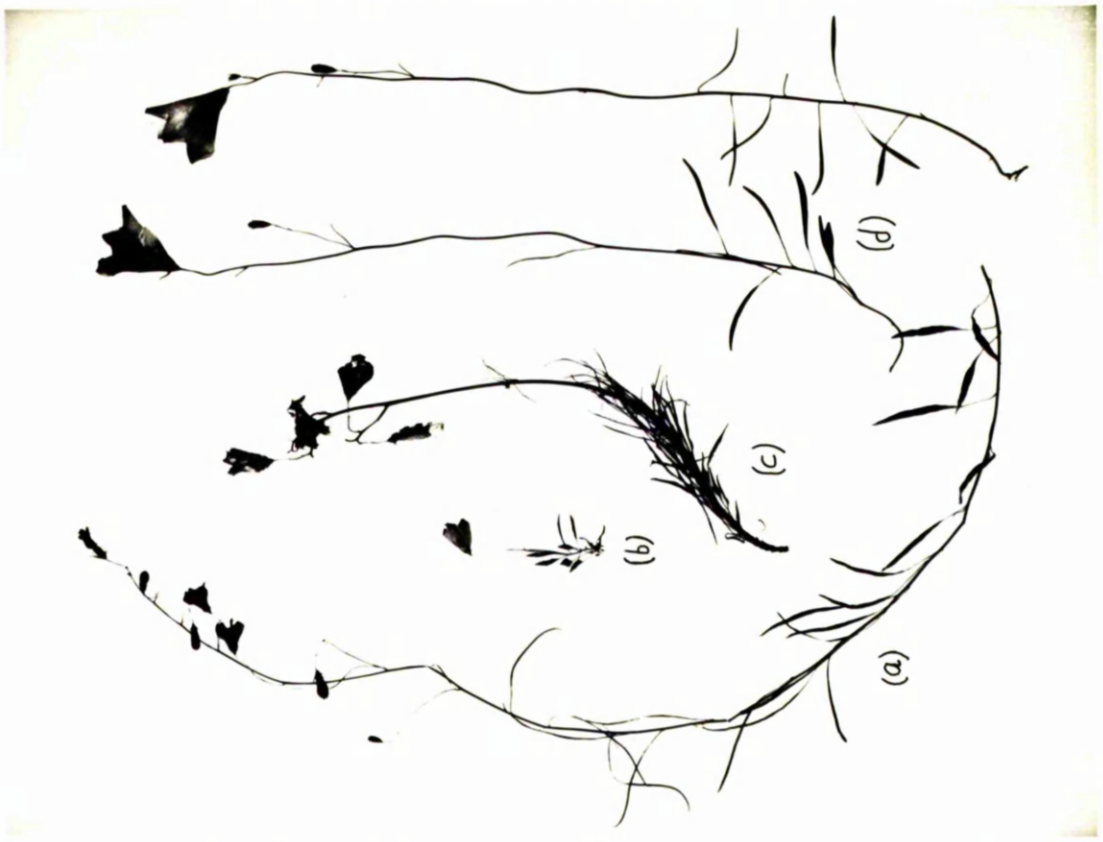


FIG. 5.5 Herbarium specimens from the wild.
(a) Lowland tetraploid (38.6) Perthshire, (b) Tetraploid from serpentine (23.6) Glendaruel, Argyll. (c) Maritime cliff hexaploid (69.7) Co. Antrim, (d) Dune hexaploid (53.7), Outer Hebrides.

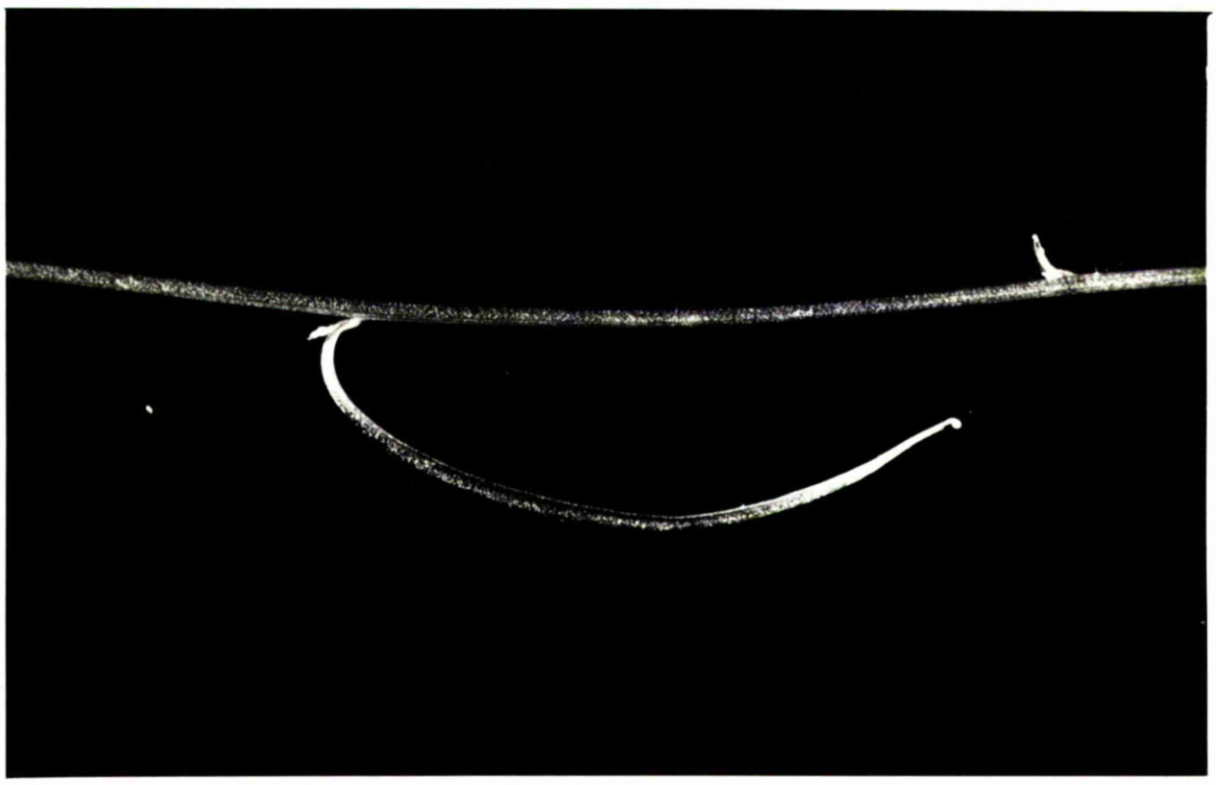


FIG. 5.6 Recurved leaf tip of Spanish hexaploid (21.7.B)

Eire. It was densely tufted as all branches of the rhizome were negatively geotropic. Neighbouring plants of the same population however had rhizomes which were, if anything, rather longer than usual, growing extensively through crevices in the rock face.

Relatively short rhizomes are a feature of the hexaploid population on the exposed seaside basalt cliffs at Easdale near Oban in Argyll (fig. 5.3) (populations 1/6, 2/6). Although in a high rainfall area, the cliffs themselves are dry and very windswept, and do not have long narrow cracks through which rhizomes might grow. The C.rotundifolia plants are confined to very small crevices, a considerable amount of rhizome often being exposed.

Hexaploid plants on the whole seem to have shorter, stouter, less vigorous rhizomes than the tetraploids.

SECTION 4 - LEAVES

In cultivation many of the hexaploids were easily distinguished in the winter vegetative condition. In contrast to the majority of the tetraploids the rosette leaves tend to be large, deep green, smoothly rounded, rigid, thick, and fleshy looking, whilst the tetraploids' rosette leaves tend to be pale green, somewhat cordate, dentate, thin and flexible. The large number of transitional leaves on the lower part of the flowering stems in many hexaploids, is already evident in early spring, and gives such plants a markedly different appearance from at least the lowland tetraploids, which have very few transitional leaves. The type of hexaploid described above also has spathulate, blunt, stem leaves, tending to crowd towards the base of the stem (fig. 5.4). Unfortunately, from the taxonomic viewpoint, montane tetraploids usually have blunt leaves, and all exposed sea-cliff populations, of whatever polyploid level, have the stem leaves crowded towards the stem base (fig. 5.5c). In addition to this, many hexaploid populations fall within the tetraploid range of variation for the above characters.

One of the Spanish hexaploids had its stem leaf tips recurved in a peculiar hook (fig. 5.6). This character was constant and characteristic of this plant. Despite a careful search no other plant was found to possess this feature.

SECTION 5 - STOMATAL SIZE

Guard cell length and number of chloroplast per guard cell are characters which often distinguish between closely related taxa at different popyploid levels (Mochizuki and Sueoka 1955, Meinl and Rothmacker 1961). Preliminary observations did not suggest that a more detailed study would be rewarding, and these characters were not examined further.

Guard cell length varied greatly within a sample from a single leaf, in some cases the existence of two size classes indicated that somatic polyploidy might have occurred. Within a guard cell it was very difficult to count accurately the number of chloroplasts, and so the attempt to use this character was abandoned.

SECTION 6 - HAIRINESS

Although tetraploids from the Cantabrian Mountains in northern Spain were completely glabrous, no completely glabrous British plants have been found.

Bielawska (1968, p.278) has shown by crosses between the usually glabrous C.polymorpha (doubtfully distinct from C.rotundifolia) and hirsute C.rotundifolia that this character was inherited in a simple Mendelian fashion with hirsuteness being dominant.

Most C.rotundifolia plants are pilose, most of the plant, except the upper part of the flowering stem and the flowers themselves, being covered with short stiff white hairs. Such hairs are usually most obvious on the lower part of the stem. The edges of the petiole and the ridges of the stem usually bear slightly larger bristles of the same type. In the reduction of hairiness these

hairs on the petiole edges and stem ridges are the last hairs to disappear. There was no obvious difference between the tetraploids and hexaploids in their degree of hairiness, though by far the hairiest plants were the two hexaploids from northern Spain. The degree of hairiness does seem to some extent to be correlated with habitat, especially in the mountains. Plants from warm dry sites are relatively hairier than those from cold damp habitats.

A particularly striking example of this was found on Ben Dorain near Bridge of Orchy, Argyll. A population (77.7) at 1050m (3500ft) on a south-west facing rock ledge had remarkably hairy basal leaves. The surrounding vegetation consisted largely of Rhacomitrium lanuginosum, Polytrichum alpinum, Silene acaulis, Dicranum fuscescens, and Galium saxatile together with 8 other flowering plant species, indicating, for this altitude, a relatively well drained and sunny habitat.

A few hundred yards away on an unstable solifluction slope in a coire at about 900m (3000ft) the plants of a neighbouring population were almost totally glabrous. The soil here was very wet, and the major species present were Polytrichum alpinum, P.urnigerum, Pellia neesiana, Nardia scalaris and Diplophyllum albicans, with occasional shoots of C.rotundifolia, Saxifraga stellaris, and Festuca vivipara being the only vascular plants present - vegetation typical of coires where the snow lies late and which often never receive direct sunlight.

A similar situation was found on a nearby mountain, Beinn Chabhair, in Glen Falloch. Here the hirsute south-facing population grow at 750m (2500ft) in Festula-Agrostis-Alchemilla alpina grassland with some Calluna on ledges, while the more or less glabrous population on the north face grew in a crevice at about the same altitude with Saxifraga nivalis.

Unfortunately the living samples taken from the above two more or less glabrous populations died before becoming established in cultivation. However some of the plants collected from about 990m (3300ft) in the north facing coire

of Aonach Beag, Ben Alder Forest, proved to be almost glabrous. These plants have grown to maturity in cultivation, and apart from one or two small hairs on the margins of the peticle base and the stem ridges, the plants are totally glabrous. However, other plants of the same population are much hairier.

There is in fact no discontinuity in degree of hairiness in the plants I have examined, the variation ranging from the totally glabrous northern Spanish tetraploids, through the Aonach Beag tetraploids with a few hairs, and the normal British tetraploids and hexaploids with pilose stems and leaves, to the Spanish hexaploids with relatively long numerous hairs.

Hair Size

It was thought at one stage that hexaploids appeared hairier than textraploids and that this might be due to longer or broader hairs. A careful examination of the hairs of cultivated plants showed that there was no major difference in hair breadth between the cytodemes, and no obvious consistent difference in hair length.

SECTION 7 - NUMBER OF FLOWERS PER STEM

Although it has been shown (Böcher 1960) that the number of flowers per stem is an extremely plastic character, under controlled conditions of cultivation a considerable genetic component has been demonstrated. C.gieseckiana, C.polymorpha and mountain topodemes of C.rotundifolia s.s. are said (Bielawska 1968, Böcher 1960) to characteristically have few flowered stems. My own observations suggest that southern and lowland plants have many flowered paniculate inflorescences with branches coming from the axils of the lower stem leaves. On the other hand northern and upland plants usually have few-flowered, racemose inflorescences, the flowering stems being unbranched except for the occasional pedicel arising from the axil of one of the uppermost leaves. A

FIG.5.7 East German diploid (48.8)

FIG 5.8. Maritime cliff tetraploid from Ben Udlaidh, Argyll.

FIG. 5.9 Maritime cliff hexaploid from Co. Antrim

FIG. 5.10 Effect of drought

(a) High altitude tetraploid. Droughted specimen on left. Right hand specimen has seven corolla lobes.

(b) Mountain rock ledge tetraploid. Two droughted specimens on left, normal on right.

diploid from the North German plain (figs. 1.1, 5.7) exemplifies the paniculate inflorescence type. Tetraploids from Ben Dourain and Beinn Udlaidh in Argyll and hexaploids from Northern Ireland (figs. 5.8, 5.9) exemplify the few-flowered racemose inflorescence type. In general the hexaploids tend to be few-flowered. The number of flowers per stem seems to be inversely correlated with flower size, plants with few-flowered stems tending to have large flowers.

SECTION 8 - HABIT

Gadella (1964) has shown that there is no correlation between habit-type and polyploid level, all three cytodemes having prostrate, erect, and lax morphodemes.

In the British material described in this work, growth habit is very clearly correlated with habitat. The growth forms described below were retained in cultivation, and indeed were often much more obvious in cultivation than in the wild.

(a) In nearly all cases the degree of branching of the inflorescences and the number of flowers per stem increased greatly in cultivation. However, tall grassland plants usually bore paniculate inflorescences, which were often mechanically weak being supported by the surrounding vegetation in the wild, but falling over when grown in pots (fig. 5.5a). This is the habit I have called lax, and corresponds to Gadella's (l.c) pendant type. This type usually have very few transitional leaves, and most of the basal leaves are usually withered by the time of flowering. Plants from upland grassland or short lowland, usually maritime grasslands have more racemose inflorescences and stronger stems which remain erect even when unsupported (fig. 5.10). The basal leaves are more persistent and there are more transitional leaves present.

(b) All sea cliff and most mountain cliff plants have short erect rigid stems with the stem leaves crowded towards the base of the stem. Basal leaves

FIG. 5.11 Maritime sea cliff tetraploid (3.8) from Argyll.

FIG. 5.12 Spanish tetraploid (23.7) from gorge.

FIG. 5.13 Mountain cliff hexaploid from Muckanaght, Connemara, Co.Galway

FIG. 5.14 Prostrate machair tetraploid (2.7) from Argyll.

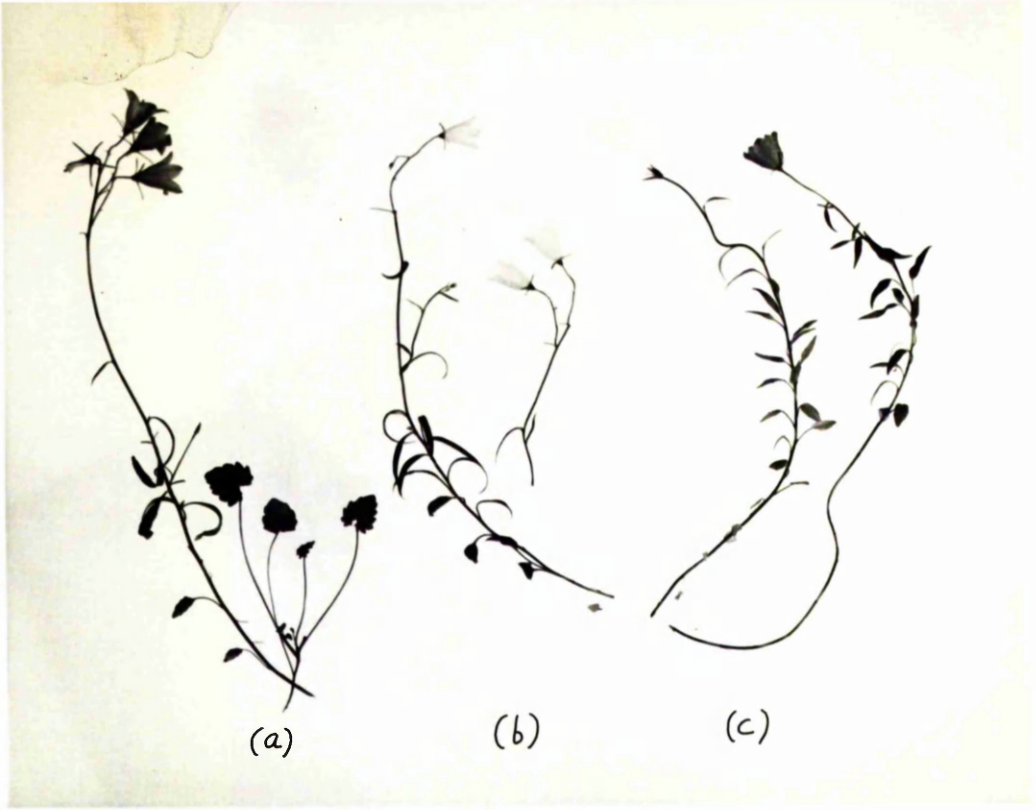


FIG. 5.15 Scottish tetraploids. (a) Maritime cliff plant (3.8). (b) White flowered plant (64.6.B). (c) Prostrate specimen from Rhacomitrium-Salix herbacea heath (44.7.A)

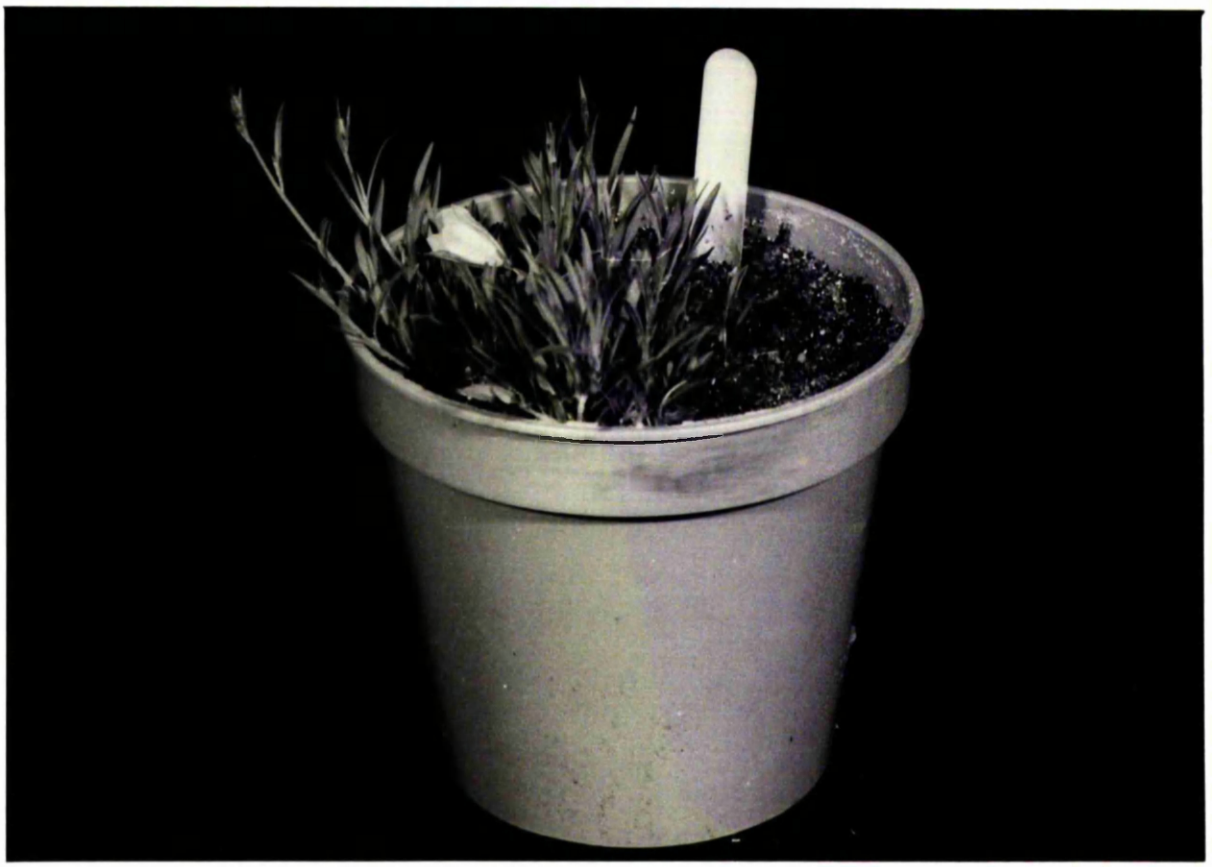


FIG. 5.16 Machair hexaploid from Colonsay, Inner Hebrides, collected in May. First short stemmed flower laid down in wild, later development morevigorous.

FIG. 5.17 High altitude Spanish tetraploid.

are prominent throughout the growing season. It seems likely that such features are adaptations to exposed cliff habitats. In some cases (figs. 1.1a, 5.11) few transitional leaves are present, while in others they are numerous (fig. 5.4).

(c) In contrast to the above, some mountain cliff plants have weak straggling stems. This habit is characteristic of all the northern Spain tetraploid populations (fig. 5.12) which are confined to rock ledges in sheltered ravines and mountain ledges. A single non-rhizomatous plant in the otherwise highly rhizomatous hexaploid population on the cliff ledges on Muckanaght in the west of Ireland has a straggling habit (figs. 5.4). This was in sharp contrast to the erect habit of the rest of the population (fig. 5.13).

(d) Prostrate and very short plants have rarely been found, and then in very exposed situations (fig. 5.5b). One heavily grazed machair population was prostrate (fig. 5.14) as was a population in Rhacomitrium-Salix herbacea heath (fig. 5.15c). Plants of these two topodemes had a very large number of transitional leaves with relatively long internodes. Machair hexaploids at Durness, Seilbost in Harris and in Colonsay bore flowers on very short stems in the wild, but given favourable conditions in cultivation could grow somewhat taller (fig. 5.16). A high altitude Spanish tetraploid topodeme from 2400m (8000ft) remained very short in cultivation (fig. 5.17).

In conclusion it can therefore be said that there is considerable ecotypic differentiation in habit in both British cytodemes. Plants from tall vegetation are tall and lax, those from exposed level situations prostrate, and those from cliffs either stiffly erect (exposed cliffs) or pendant (sheltered cliffs and ravines).

SECTION 9 - FLOWER SIZE AND SHAPE

Flower size is sometimes used as a taxonomic character in the Heterophylla (Kovanda 1970c) and as a guide to polyploid level in C.rotundifolia s.s. and

FIG. 5.18 Lowland tetraploid from Aviemore, Inverness-shire. Three specimens from wild on right, cultivated specimen on left.

FIG. 5.19 The effect of damage to stem on flower size. The lowest two flowers are on a branch inserted below point of damage which appears as a white mark on the stem. The smaller upper flowers are borne above the point of damage.

C.gieseckiana (Böcher 1960). On the whole diploids are said to have smaller flowers than closely related polyploids. This idea guided much of my early field collecting in the hunt for British diploids, especially in the sandy heaths of the eastern Highlands of Scotland where great variation in flower size was noted. In this area the populations often seemed to be divided into two types of plant. There were fairly large specimens with more or less paniculate inflorescences and large deep blue flowers. Among those, particularly in areas of dry soil, grew smaller more rigid plants with spike-like inflorescences and small very pale blue flowers with even paler areas between the veins of the corolla. These plants often had protruding stigmas (a character of C.hispanica) and flowers which withered very rapidly after collection. It was initially thought that these populations might be mixtures of tetraploids and diploids, but in cultivation the second small-flowered variant became similar to the first type (fig. 5.18) and all plants proved to be tetraploid. Thus it was concluded that the initial difference in appearance was due to environmental factors, of which drought seemed the most probable.

To test this possibility, several plants were split into two and grown side by side in a cold frame in pots. Both pots of each clone were watered adequately till they began to flower, then the watering of one of each pair was reduced as much as possible without causing the plant to wilt too severly. The droughted plants did produce smaller flowers with protruding stigmas on shorter stems (figs. 5.4, 5.10), and in one case an abnormally highly dissected flower was formed (fig. 5.4 extreme right)

On a stem which was bent but not broken, the flowers which developed above the point of damage were smaller and much paler than those borne below (fig. 5.19). The damage would probably restrict the flow in both xylem and phloem, so the small size of the upper flowers could be the result of lack of water, lack of nutrients, or a combination of both.

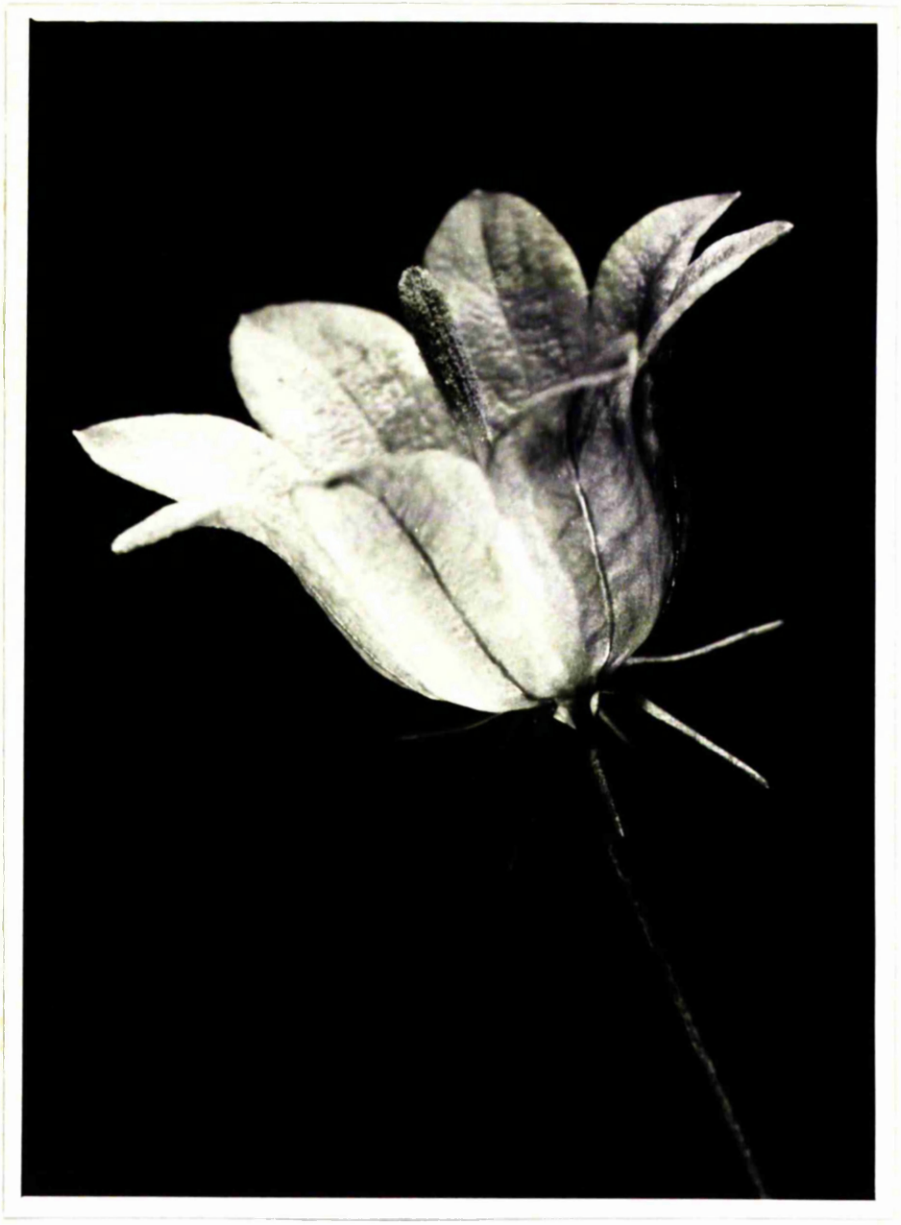


FIG. 5.20 Lateral view of pleiomerous flower of plant 51.6.B from Girvan, Ayrshire. Floral formula $K_8\ C_{(8)}\ A_8\ \underline{G}_4$

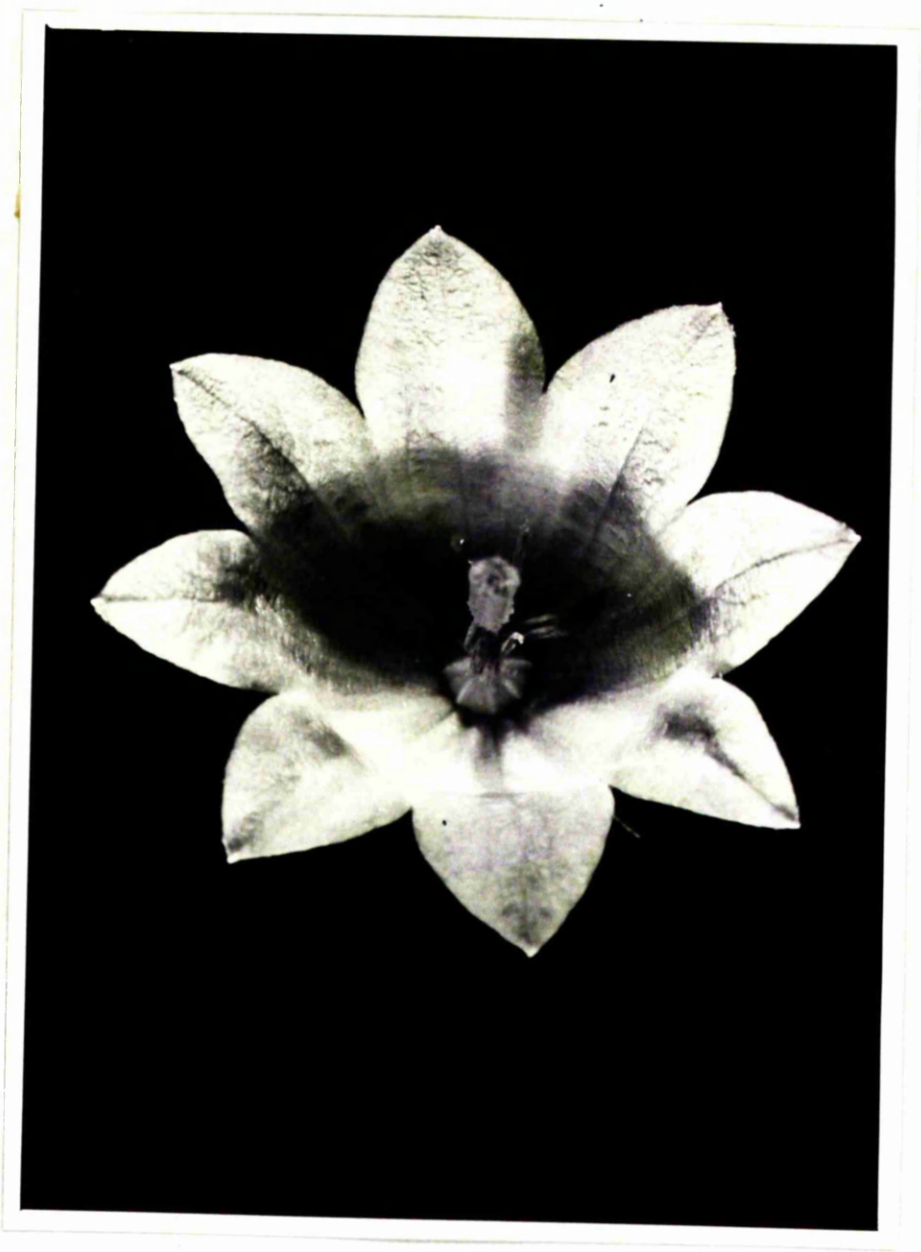


FIG. 5.21 Face view of pleiomerous flower shown in fig. 5.20

FIG. 5.22 Normal flower and male sterile "double" flower with petaloid anthers from a plant from Glendaruel, Argyll (25.6)

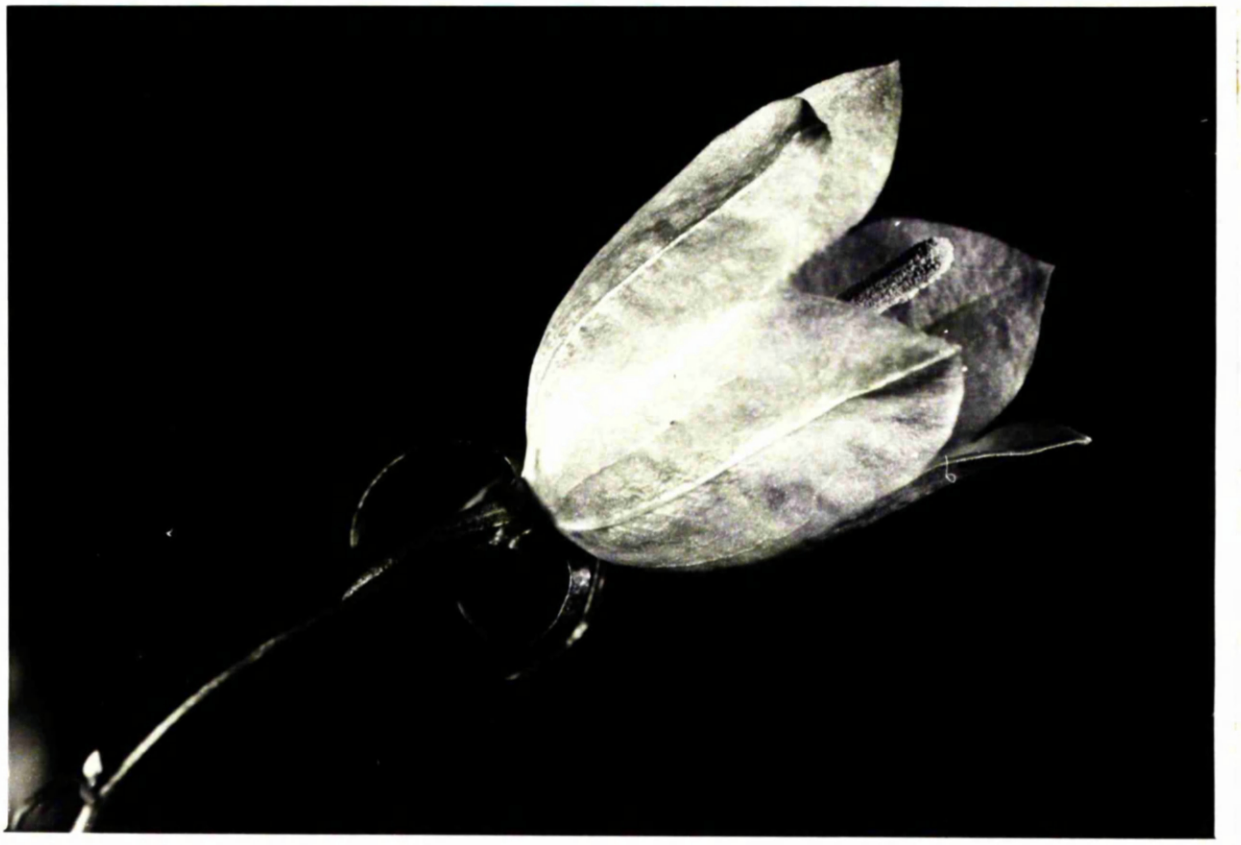


FIG. 5.23 Flower with straight corolla lobes of hexaploid plant 75.7.A from Ben an Lochain, nr. Arrochar, Argyll.

The position of a flower on the stem can also have a bearing on its size and the numbers of floral parts. As described for Greenland plants by Böcher (1960), high altitude British tetraploids and many hexaploids often have six corolla lobes in the leading flower of many stems. Lateral flowers on the same stems usually have the normal 5-lobed corollas. A lowland specimen (51.6.B) always bore leading flowers with the floral formula $K_8\ C_{(8)}\ A_8\ G_{\overline{4}}$ (figs. 5.20, 5.21). If lateral flowers were present the uppermost lateral flower often had 6 or 7 corollas lobes, but the corollas of the lower laterals were 5-lobed.

The lateral flowers of some genotypes frequently had fewer than 5 corolla lobes, though the corolla length of these flowers was no less than that of the leading flower. This feature was particularly noticeable on a white flowered plant (64.6.E), whose lateral flowers often had the floral formula $K_{3-4}C_{(3)-(4)}$ $A_{3-4}G_{\overline{2}}$.

The tendency for a plant to have flowers with more or fewer than the normal number of parts in certain regions of the inflorescence is genetically controlled. All plants showing such characteristics were constant in displaying them over several years and in cultivation under different conditions.

Although not observed in the course of this study, a teratological form of C.rotundifolia with free petals has been reported from Switzerland (quoted in Kovanda 1970a). Two small slender stems each bearing a single flower with five free petals collected on Freshwater Down in the Isle of Wight in 1897 are preserved in the British Museum. Whether this variant is phenotypic or genotypic is unknown.

Two plants (Nos. 25.6.H and 38.6.H) occasionally bore flowers with petaloid stamens which contained no pollen (fig. 5.22). These were nearly always lateral flowers, but only a small proportion of the laterals were modified in this way. If the frequency of male sterile flowers could be increased either by modifying the environment or by breeding a plant with a higher proportion of

FIG. 5.24 Mountain hexaploid from the Merrick, Kircudbrightshire. (13.8.C)

FIG. 5.25 Flower of Spanish Hexaploid 21.7.B

the "double" male sterile flowers, such plants could be very useful for breeding experiments.

The degree of dissection of the corolla has often been measured in quantitative studies of C.rotundifolia and its allies (Bielawska, 1964, Kovanda 1970a), but the results were of no great taxonomic significance. Observations on the plants of my collection suggested that the range of variation in both the tetraploids and hexaploids was much the same. Also, droughting could affect the degree of dissection (fig. 5.4).

The degree to which the corolla lobes are recurved is very constant and characteristic for a genotype, but observation suggested that this character was so variable within a cytodeme that it could not be used to distinguish tetraploids and hexaploids. The extremes of the range of variation are best illustrated by two hexaploids. A Scottish mountain hexaploid plant from Argyll (75.7.A) has lobes which are hardly recurved at all, (fig. 5.23), while the hexaploid from the Merrick, Kircudbrightshire (13.8.C)(fig. 5.24) has highly recurved lobes.

The overall shape of the corolla is to a large extent controlled by the form of the base of the corolla, but with the length to breadth ratio playing a part. The corolla base varies from hemispherical (figs. 5.23, 5.24), giving a cup or deep saucer shaped corolla, to gradually tapering (fig. 5.25), giving a trumpet shaped corolla. The form of the corolla base (and ovary) is difficult to determine from herbarium specimens. The hemispherical corolla base is usually associated with a relatively short broad corolla and a hemispherical ovary. This character combination is a diagnostic feature of C.gieseckiana and is usually found in plants from northern and high altitude localities in the British Isles and northern Spain, whether the plants be tetraploid or hexaploid. A plant with a tapering corolla base usually also has a relatively long narrow trumpet-shaped flower and an ovary which tapers into the flower-stalk (fig.5.25).

SECTION 10 - FLOWER COLOUR

The flower colour of C. rotundifolia is usually described as blue, and bluebell is a frequent name of the species in several language (e.g. Bluebell of Scotland, Bláklukka in Icelandic, Blaaklokke in Danish). However the flower colour does vary considerably, from white through all shades of pale blue to a deep blue, and sometimes even a violet blue. White flowered plants occur rarely throughout the range of the species (Clapham et. al 1962) and I have seen specimens from Scotland, Iceland and East Greenland. The flower colour of 38 blue-flowered plants was therefore matched with the colours in the Royal Horticultural Society's colour chart to see if examination would reveal any consistent differences between cytodemes or topodemes, or any clinal variation (Table 5.1). The plants examined were chosen to represent the range of flower pigmentation found in the collection, and so probably cover most of the variation shown by, at least, British specimens.

The colour code is such that as the number increases from 85 to 94 the amount of violet decreases and the colour becomes a more true blue. The letters after the number signify the intensity of the pigmentation, A denoting the deepest colour and D the palest.

The flowers of the Spanish tetraploids had much more violet in their corolla pigmentation than plants from elsewhere. Also they all have a relatively deep pigmentation, falling into the categories 85A and 87A. The rather different looking high altitude Spanish tetraploids have flowers of the same general colour, but of a lighter hue (87B). Slightly less violet flowers are found in the East German diploid and an Austrian tetraploid (88B). The other plants, which were all British, have flowers of a much truer blue, falling into the categories 90D, 91A B C, 92A B and 93A B C D. No. 21.7.B, the Spanish hexaploid, had flowers of the colour 94C.

These data suggest that there are definite geographical differences in

TABLE 5.1

FLOWER COLOUR AS MATCHED AGAINST ROYAL HORTICULTURAL SOCIETY COLOUR CHART

(As the number increases from 85 to 94 the colour changes from violet blue to a truer blue, (A) denoting a deep pig mentation, (B) (C) and (D) denoting progressively lighter pigmentation)

Flower Colour	Plants
85A	1 Spanish 4x
87A	1 Spanish 4x
87B	High altitude Spanish 4x
88B	E.German 2x, 1 Austrian 4x
90D	1 Scottish 6x
91A	3 British 4x, 3 British 6x
91B	1 British 4x
91C	1 Irish 6x
92A	4 British 4x, 5 British 6x
92B	1 Irish 6x
93C	1 British 4x
94A	1 Irish 6x
94B	1 British 4x, 2 British 6x
94C	4 British 4x, 2 British 6x
94D	1 British 6x, 1 Austrian C.cochleariifolia

flower colour, with British plants being of a much truer blue than specimens from Spain, Austria and Germany. This result is backed up by further observations on wild and cultivated material of other populations from Spain, Austria, the Black Forest and Munich. The Spanish tetraploid populations in particular stand out through their having a relatively uniform deep violet colour similar to that of C.scheuchzeri and the tetraploid Spanish C.ficarioides. At the other end of the scale the plant with the lightest blue flower, an Isle of Man hexaploid, has the same flower colour as an Austrian plant of C.cochlearifolia.

SECTION 11 - POLLEN COLOUR

Pollen colour has occasionally been noted in members of the C.rotundifolia complex. Böcher (1960 p.59), describes all Greenland plants as having white pollen. I classified a number of plants into 5 pollen colour classes:- cream (probably the same as Böcher's white), very pale mauve, pale mauve, mauve, and deep mauve (table 5.2). Except that white flowered plants always had cream coloured pollen, presumably because they totally lacked anthocyanins, there was no correlation between flower colour and pollen colour. There was also no correlation between the polyploid level and/or geographical origin and pollen colour, and the variation within a single topodeme was sometimes considerable. Among the tetraploid topodemes, that from Fleam Dyke near Cambridge (1.7) had a range from pale to deep mauve, while that from Ardlamont Point in Argyll varied from cream to mauve. The hexaploids behaved in the same way, an Isle of Man population varying from cream to mauve, and one from Strontian, Argyll from very pale mauve to mauve. The one Greenland diploid in my possession has very pale mauve pollen. Pollen colour might prove to be a useful character for genetic analysis.

TABLE 5.2

POLLEN COLOUR

Colour	British tetraploids	British Hexaploids	Others
Cream	9	3	
Very pale mauve	4	4	Greenland diploid
Pale mauve	19	10	
Mauve	22	19	Spanish hexaploids Canadian hexaploid East German diploid
Deep mauve	1	1	

SECTION 12 - OVARY SHAPE

The ovary shape is best examined in the bud stage, and varies from conical to hemispherical.

Observations on British tetraploids have led me to postulate that a hemispherical ovary is usually associated with a hemispherical corolla base, and is most frequent in plants from northern and upland areas.

By far the most strikingly hemispherical ovaries are however found in hexaploids from extremely harsh habitats such as the very exposed sea cliffs at Easdale in Argyll (fig. 5.4), and the mountain summit plateaux of the Merrick (fig. 5.24) and Ben Alder. A hexaploid from Ben an Lochain, Argyll which occurred in an otherwise tetraploid population had ovaries which were markedly more hemispherical than those of the surrounding tetraploids. Hexaploids from one of the most extreme habitats in which I have seen C.rotundifolia growing, namely beside a semi-permanent snow patch at 1000m (3000ft) on Aonach Beag in the Nevis range, ... had conical ovaries. Hexaploid populations from other, less extreme, environments have the same sort of range of variation in ovary shape as the tetraploids though there is usually a preponderance of individuals with more or less hemispherical ovaries. Where the ovary is hemispherical it is broader than long, and this is the key character usually used to define C.gieseckiana. Podlech has identified a number of British specimens in the herbarium of the Royal Botanic Garden, Edinburgh as C.gieseckiana, solely, I believe, as a consequence of their having more or less hemispherical ovaries (see Chapter 3). I think it is impossible to believe that they could belong to a separate species, genetically isolated from the surrounding C.rotundifolia populations. My observations on the specimens have led me to believe that they do not differ in any consistent way from C.rotundifolia, and from their geographical locations I should expect them all to be tetraploids.

SECTION 13 - POLLEN DIAMETER

(a) Introduction

Pollen grain diameter has been claimed to be the most reliable single character for the separation of diploids, tetraploids and hexaploids in C.rotundifolia and related species (Kovanda 1970a, Böcher 1960). Kovanda points out that pollen size can only be a guide to polyploid level in comparisons between presumed closely related cytodemes.

Between what are presumed to be related taxa from very different geographical localities pollen size may be an unreliable guide to chromosome number. However within a limited geographical area it is often a good indication of polyploid level. Böcher (1960) describes how the Greenland diploids and tetraploids can be fairly reliably distinguished by pollen grain size, as can the European diploids and tetraploids. However the Greenland diploids have pollen of much the same size as the European tetraploids.

In general it is usually assumed that the pollen grain size of a species is very constant, being little influenced by external factors, and more or less proportional in volume to the amount of D.N.A. present. A good deal of work on factors affecting pollen size is reported in the literature. Liskens (1964) states that apart from genetic factors (many genes have an effect on pollen size), environmental factors such as water and mineral supply have an effect on pollen size. Schoch-Bodmer (1940) reports a difference in pollen size between main and lateral flowers in Lythrum salicaria. He also quotes earlier works recording reduced pollen size with low temperature in Linaria genistifolia, and Antirrhinum majus, and towards the end of the season (late October) in Oenothera. Further work on temperature by Kurtz and Liverman (1958) showed that pollen diameter decreased at high and low night temperatures in tomato and cocklebur (Xanthium canadense), and at high day temperatures in cocklebur. Mikkelsen (1949) however, attempting to study the effect of

TABLE 5.3

Temperature	Pollen diameter with standard deviation
15°C	65 ± 1.4
22°C	72 ± 1.6
29°C	61 ± 1

TABLE 5.11 THE TESTA CELL WIDTH OF 24 CLONES GROWN UNDER UNIFORM CONDITIONS (THE FIGURES GIVEN ARE THE MEANS OF 10 CELLS FROM 2 SEEDS OF EACH CLONE, AND THE 95% CONFIDENCE LIMITS)

e No	Ploidy level	Locality	Testa cell width, u	95% confidence limits
6.A	4x	Arrochar	2.07	0.57
.6.B	4x	Derbyshire	2.29	0.35
.6.B	6x	Carrbridge	2.40	0.17
.6.B	4x	Muir of Ord	2.72	0.41
.6.C	4x	Suffolk	2.79	0.39
.7.A	4x	Bridge of Orchy, Argyll	2.86	0.36
.8.C	4x	Aberdeen	2.86	0.36
.7.A	6x	Arrochar	2.93	0.39
.6.B	4x	Campsies	3.07	0.59
.8.B	6x	Inveran, Southerland	3.22	0.64
.7.C	4x	Cambridge	3.15	0.73
.8.A	6x	Connemara	3.29	0.70
.8.B	4x	Tighmabruaich, Argyll	3.58	0.63
.7.A	4x	Bridge of Orchy	3.72	0.28
.7.C	6x	Co. Clare	4.22	1.11
.8.C	4x	Carrbridge	4.36	0.68
.8.D	6x	Co. Mayo	5.01	0.55
.7.N	6x	Harris	5.43	0.84
.7.A	6x	Lizard	5.43	0.92
.8.D	6x	Connemara	5.93	1.09
.8.D	6x	Co. Sligo	6.65	1.27
.6.C	6x	Oban	6.86	0.81
.8.C	4x	Norfolk	7.01	1.06
.8.D	6x	Mull	7.29	1.18

temperature on pollen size in Pelagonium zonale came to the conclusion that nutrition was a most important factor, temperature affecting the growth of the plants, and thus the nutrition of the developing pollen. His results are given in table 5.3.

The plants at 15°C and 29°C were growing poorly. It can be seen that the differences between the highest and lowest averages (61 and 72) is 18% of the lowest.

If it is assumed that the volume of a pollen grain is proportional to the amount of D.N.A. it contains the expected differences in the diameters of the pollen grains of diploid, tetraploid and hexaploid cytodemes are shown in table 5.4. The 18% difference in diameter caused by environmental factors in the above experiment can be compared with the calculated increase in pollen diameter of an autotetraploid over its diploid parent of 26%, and a diameter increase from tetraploid to hexaploid of only 14.5% of the tetraploid pollen diameter. It can therefore be seen that environment alone might cause an autotetraploid to have smaller pollen than its diploid parent, if the diploid were growing in favourable conditions and the tetraploid in unfavourable conditions. This problem could be overcome to a certain extent by growing plants whose pollen size is to be compared in a similar favourable environment, but it points to the dangers involved in drawing too definite conclusions from pollen from herbarium specimens (c.f. the suggestion by Böcher 1960 that diploids were probably present on the Isle of Wight and at Oxford).

My object in investigating pollen size was primarly to find out if it could be used to separate tetraploids and hexaploids, but a few observations were also made on the effect of the position of a flower on a raceme and environmental factors.

TABLE 5.4

THE RELATIONSHIP BETWEEN THE DIAMETERS OF SPHERES WHOSE VALUMES DIFFER BY FACTORS OF 2 AND 3

(i.e. the expected size differences between diploid, tetraploid and hexaploid pollen grains if their volume is proportionate to the amount of D.N.A. present).

Ratio of volumes of spheres	1	:	2	:	3
Ratio of diameters	$\sqrt[3]{\frac{3}{4\pi}}$	:	$\sqrt[3]{\frac{6}{4\pi}}$	:	$\sqrt[3]{\frac{9}{4\pi}}$
=	100	:	126.0	:	144.2

Therefore the diameter of tetraploid pollen would be expected to be 26% greater than that of a diploid, and hexaploid pollen 14.5% greater than that of a tetraploid.

(b) Methods

2 ramets each of 30 clones (1 diploid, 14 tetraploid, and 15 hexaploid) were potted up using the same compost in 6 inch plastic pots and spaced about 4 inches apart in 2 random blocks, each block containing one ramet of each clone. Each block was surrounded by similarly potted plants to negate any edge effect. The plants were allowed to grow undisturbed in the greenhouse for ten weeks, during which period they made rapid growth and flowered. Herbarium specimens were then taken from each plant and, when dry, the pollen from a strong lateral bud measured, without pretreatment, in 200 m.c. silicone oil using an oil immersion lens. Concurrently, pollen from other herbarium specimens was measured in the same way to investigate position and environmental effects. In each sample 50 grains were measured.

The results were calculated with the aid of a KDF9 computor.

(c) Results

(i) Position effect

The results in table 5.5 suggest that the position of a flower on a stem has little effect on pollen size, even though in the case of plant 51.6.B it had a marked effect on the number of floral parts.

(ii) Environmental effects

No obvious general trend can be noticed in pollen size between the different environments. The droughted and shaded plants had pollen which was sometimes slightly larger, sometimes smaller than that of the greenhouse grown plants, despite the very much smaller flowers of the droughted plants. Plants from the wild had pollen of much the same size as greenhouse grown plants, or at least this is suggested by the two results obtained despite the gross difference in habit (fig. 5.18).

Two of the plants grown outside in full sun have obviously larger pollen than ramets of the same class grown indoors. The opposite result was obtained with a similarly treated 3rd clone, but the outside ramet (with the smaller

TABLE 5.5 THE EFFECT OF FLOWER POSITION AND ENVIRONMENT ON POLLEN SIZE

Code No. of plant	Polyploid level	Greenhouse		In pots outside
		Lateral	Terminal	
51.6.B *	4x	32.46 ±0.49	33.40 ±0.58	"
55.6.a	6x	33.17 ±0.49	33.92 ±0.49	"
100.6.A	6x	33.10 ±0.42	"	30.11 ±0.28
61.7.A	6x	29.22 ±0.34	"	33.02 ±0.38
93.6.A	6x	29.32 ±0.42	"	32.94 ±0.55

*The diameter of pollen of this plant from the wild was 32.42±0.57

TABLE 5.6 THE EFFECT OF TWO DIFFERENT ENVIRONMENTS ON POLLEN SIZE

Code No of plant	Polyploid level	Pollen diameter in u.m. with 95% Confidence Limits	
		Experimental layout in Greenhouse	In cold frame drought ed and shaded
46.6.A *	4x	28.77 ±0.30 29.33 ±0.40	31.82 ±0.44
77.7.A	4x	29.39 ±0.63 29.92 ±0.80	29.43 ±0.52
6.6.A	4x	30.95 ±0.38 32.21 ±0.49	29.95 ±0.45
1.6.C	6x	28.58 ±0.31 31.68 ±0.45	32.71 ±0.55 32.89 ±0.47
59.7.C	6x	30.73 ±0.38 35.70 ±0.44	33.97 ±0.43
75.7.A	6x	34.67 ±0.50 35.12 ±0.49	35.82 ±0.41

* The diameter of pollen of this plant from the wild was 28.27±0.34

pollen) was very weak and unhealthy.

A few tentative conclusions may be drawn from the above results. There is a suggestion that the largest pollen will be produced by vigorous plants grown outdoors. Adverse conditions (e.g. drought and shade), even of 2 months duration, do not seem to have much effect on a vigorous plant. However a weak plant (i.e. with thin spindly single flowered stems) will probably have small pollen grains, irrespective of whether the weakness has been the result of competition in the wild or waterlogging in a pot.

(iii) Genetic effect

The results of the experimental blocks described above are given in graphical form in fig. 5.26 and the figures in table 5.7.

It can be seen that the one diploid plant has much smaller pollen than any other. However, a good separation of tetraploids and hexaploids was not obtained, though the tetraploids did tend to have smaller pollen than the hexaploids. Of the 29 tetraploids and hexaploids, the plants with the 7 lowest means are tetraploids, and those with the 9 highest means are hexaploids.

(d) Discussion and conclusions

The above results show that pollen size, at least on its own, is not a very reliable indication of polyploid level.

The most remarkable result is the low and fairly constant variation in size of the pollen from a single flower. This is to be contrasted with the great variation which may occur between different flowers of the same clone (e.g. 59.7.A). Within a clone there is no obvious correlation with other floral characters, two large flowers often having pollen of different sizes while small and large flowers may have pollen of the same size.

(i) Giant pollen grains

Giant pollen was seen in several samples of both tetraploid and hexaploid plants, reaching a frequency of about 40% in plant 51.6.B. These grains, which

TABLE 5.7 THE POLLEN GRAIN SIZE (DIAMETER) OF 30 GENOTYPES GROWN UNDER UNIFORM CONDITIONS

Code No.	Ploidy level	Locality	Mean pollen diam. of 2 samples of 50 grains	Mean Diam. and 95% confidence limits of sample (1)	Mean Diam and 95% confidence limits of sample (2)
48.8.A	2x	East Germany	25.90	25.64±0.28	26.16±0.35
86.6.C	4x	Suffolk	28.18	27.65±0.46	28.71±0.57
41.6.B	4x	Muir of Ord	28.87	28.85±0.48	28.88±0.38
3.7.B	4x	Tighnabruaich, Argyll	29.00	28.10±0.39	29.83±0.56
1.7.C	4x	Cambridge	29.06	28.71±0.44	29.41±0.43
46.6.A	4x	Aviemore	29.06	28.77±0.30	29.33±0.40
80.6.B	4x	Derbyshire	29.21	28.14±0.38	30.28±0.37
77.7.A	4x	Bridge of Orchy, Argyll	29.66	29.39±0.63	29.92±0.80
1.6.C	6x	Oban	30.13	28.58±0.31	31.68±0.45
84.8.C	4x	Aberdeen	30.23	29.61±0.51	30.84±0.46
31.7.C	6x	Co. Clare	30.47	29.11±0.44	31.83±0.40
16.8.A	6x	Connemara	30.69	29.95±0.39	31.43±0.41
64.6.B	4x	Campsies	30.83	29.37±0.37	32.29±0.38
21.8.B	6x	Jura	30.95	29.61±0.43	32.29±0.40
44.7.A	4x	Bridge of Orchy, Argyll	31.56	30.45±0.54	32.67±0.38
6.6.A	4x	Arrochar	31.58	30.95±0.38	32.21±0.49
20.8.B	6x	Co. Mayo	31.69	30.80±0.40	32.57±0.46
64.8.C	4x	Norfolk	31.89	31.82±0.54	31.96±0.51
101.6.H	6x	Isle of Man	32.25	31.96±0.46	32.53±0.45
60.6.C	4x	Aberystwyth	32.31	31.46±0.33	33.16±0.34
68.8.C	4x	Carrbridge	32.49	32.43±0.53	32.55±0.38
16.8.D	6x	Connemara	32.71	31.73±0.39	33.68±0.47
45.6.B	6x	Carrbridge	33.06	32.78±0.52	33.33±0.48
19.8.D	6x	Co. Sligo	33.20	32.29±0.44	34.11±0.62
59.7.A	6x	Lizard	33.22	30.73±0.38	35.70±0.44
83.8.D	6x	Teesdale	33.78	33.78±0.41	
77.8.B	6x	Inveran, Sutherland	33.85	33.20±0.42	34.50±0.39
31.8.D	6x	Mull	34.17	33.33±0.44	35.01±0.52
75.7.A	6x	Arrochar	34.90	34.67±0.50	35.12±0.49
53.7.N	6x	Harris	37.92	35.86±0.53	39.97±0.44

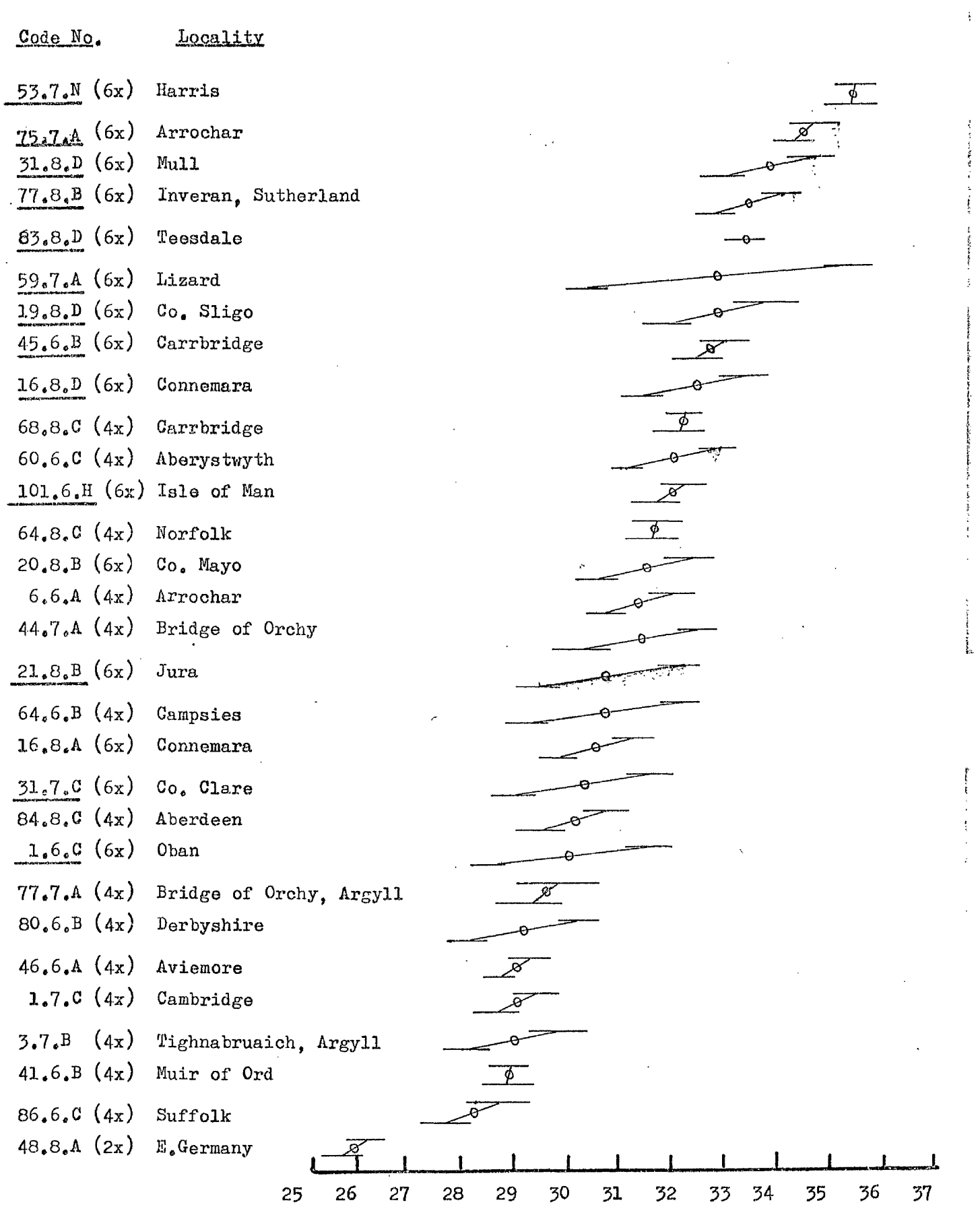


FIG. 5.26 The pollen diameters of 30 plants (1 diploid, 14 tetraploid, 15 hexaploid). The code numbers of the hexaploid plants are underlined. Each horizontal line represents the 95% confidence limits for the diameters of 50 pollen grains. In all but one case measurements for one flower from each of two ramets of each clone are given, together with the mean for that clone (circled).

were omitted from the above samples, were very obviously larger than the majority of the pollen grains and were probably the result of the malfunctioning of meiosis giving rise to pollen with the unreduced chromosome number.

(ii) Comparison with other workers' results

In comparison with other workers' results, the pollen measurements given above are rather small. This is probably because Böcher (1960), Gadella (1964) and Kovanda (1970a) pretreated their pollen and mounted it in glycerine. This technique has been criticised by Andersen (1960).

SECTION 14 - SEED SIZE

Seed size has been used to distinguish between diploids and tetraploids (Böcher 1960, Kovanda 1970), so it was therefore decided to make measurements to find if this character was of any help in distinguishing between the tetraploid and hexaploid cytodemes in Britain.

The length and breadth of 10 seeds from each sample were measured at a magnification of X100.

Most of the seed samples were taken from the plants used in the study of pollen size, but some samples were also taken from plants of some of the same clones growing in another greenhouse to examine variation within a clone. The results were calculated using modifications of the computer programme used to calculate the data on the pollen measurements.

From table 5.8 it can be seen that length alone gives virtually no guide to the polyploid level of the plant on which the seed was formed. This is also true of breadth alone and the length to breadth ratio.

Length x breadth gives some separation, the hexaploids having higher values than the tetraploids. However, a tetraploid from Thetford (64.8.C) has large seeds well within the hexaploid size range, and the hexaploid from Ca Clare (37.7.C) has small seeds, about the same size of those of many of the tetraploids.

TABLE 5.8 THE SEED DIMENSIONS OF 22 CLONES GROWN UNDER UNIFORM CONDITIONS (THE FIGURES GIVEN ARE THE MEANS OF 10 SEEDS AND THE 95% CONFIDENCE LIMITS)

Code No.	Ploidy level	Locality	Length X Breadth sq.μm x 10^3	Length / Breadth	Length μm	Breadth μm
3.7.B	4x	Tighnabruaich, Argyll	24.3±1.4	1.65±0.10	728±33	423±16
41.6.B	4x	Muir of Ord	26.6±1.7	2.03±0.05	844±34	416±13
86.6.C	4x	Suffolk	27.1±1.1	2.02±0.14	853±22	422±20
6.6.A	4x	Arrochar	28.5±2.0	2.36±0.11	943±44	400±15
1.7.C	4x	Cambridge	30.1±1.6	2.12±0.14	918±38	434±16
84.8.C	4x	Aberdeen	30.1±1.0	2.12±0.09	918±26	434±12
68.8.C	4x	Carrbridge	30.1±2.5	2.43±0.14	980±36	407±24
31.7.C	6x	Co. Clare	31.2±1.6	2.23±0.09	971±36	436±13
77.7.C	4x	Bridge of Orchy, Argyll	31.5±1.1	2.65±0.11	1050±15	397±14
20.8.B	6x	Co. Mayo	31.9±1.4	2.25±0.15	971±39	435±18
64.6.B	4x	Campsies	32.2±1.7	2.14±0-09	955±38	447±12
16.8.A	6x	Connemara	32.8±2.8	2.55±0.21	1047±52	414±27
53.7.N	6x	Harris	33.0±1.8	1.78±0.09	878±12	497±26
19.8.D	6x	Co. Sligo	33.1±1.7	1.96±0.06	921±25	475±15
1.6.C	6x	Oban	33.3±2.1	1.75±0.09	875±20	502±26
21.8.B	6x	Jura	33.4±1.3	1.95±0.10	928±34	477±13
59.7.A	6x	Lizard	35.0±1.5	2.44±0.11	1062±33	436±13
64.8.C	4x	Norfolk	36.0±3.8	1.93±0.12	957±71	495±21
16.8.D	6x	Connemara	36.0±1.5	2.24±0.12	1033±36	462±18
75.7.A	6x	Arrochar	36.5±2.8	2.71±0.20	1143±75	423±14
77.8.B	6x	Inveran, Sutherland	36.5±2.8	2.66±0.15	1141±36	432±19
45.6.B	6x	Carrbridge	37.3±2.0	2.08±0.11	1010±30	488±22

SECTION 15 - SEED WEIGHT

Although seed linear measurements have frequently been used in attempts to separate closely related plants of different polyploid levels, I have found no references to efforts to use the most integrated measure of seed size - namely seed weight.

(a) Method

Ten seeds of each of 19 of the genotypes grown under standard conditions were weighed accurately on a Mordue Microbalance. To detect any effect variation in environmental conditions might have on seed size, samples of 50 seeds were weighed from two ramets of a clone which had been growing in different greenhouses. Each sample was weighed in lots of 10 seeds to reveal the range of variation to be expected between successive samples (also, the balance was so sensitive that no more than 10-12 seeds could be weighed at a time).

(b) Results and discussion

Although it is evident that there is some variation between such small samples (table 5.9), it is considered that a sample size of 10, though small, is adequate. The results in table 5.10 show that although tetraploids tend to have lighter seeds than hexaploids there is quite a large area of overlap. This was obvious even to the naked eye as seeds of the hexaploids 16.8.A and 31.8.D were noticeably smaller than those of some of the tetraploids. It must be remembered, too, that these plants were growing under uniform conditions. Table 5.9 shows the great variation which can be induced by environmental factors.

Thus, though seed weight might give some indication of the polyploid level of plants growing under uniform conditions, environmental variation is likely to render it useless as a character to separate seed samples collected in the wild.

TABLE 5.9 VARIATION IN SEED WEIGHT BETWEEN RAMETS OF A CLONE GROWING UNDER DIFFERENT CONDITIONS

Tetraploid clone 6.6.C from near Arrochar in Argyll:

	Warm Greenhouse	Cool Greenhouse
Average weight per seed of successive samples of 10 seeds (in μg)	58.0	83.3
	62.0	79.0
	65.45	86.8
	65.2	81.1
	58.4	83.2
Average weight per seed of 50 seeds:	61.81	82.68

Tetraploid clone 86.6.C from Cavenham Heath, Suffolk:

	Warm Greenhouse	Cool Greenhouse
Average weight per seed of successive samples of 10 seeds (in μg)	60.8	71.27
	67.2	72.4
	68.4	71.86
	65.3	69.8
	64.7	67.5
Average weight per seed of 50 seeds:	65.28	70.59

TABLE 5.10 COMPARISON OF SEED WEIGHTS OF TETRAPLOIDS AND HEXAPLOIDS

Code No.	Ploidy level	Locality	Average weight per seed of 10 seeds in u.g.
3.7.B	4x	Tighnabruaich, Argyll	56.0
41.6.B	4x	Muir of Ord, Ross and Cromarty	56.0
6.6.A	4x	nr. Arrochar, Argyll	58.0
86.6.C	4x	Cavenham Heath, Suffolk	69.4
16.8.A	6x	Connemara, Co. Galway	70.0
84.8.C	4x	Aberdeen	76.0
31.8.D	6x	Mull, Argyll	76.0
64.6.B	4x	Carron Valley, Stirlingshire	78.6
68.8.C	4x	Carrbridge, Inverness	80.0
20.8.D	6x	Pontoon, Co. Mayo	80.0
1.7.C	4x	Cambridge	81.0
75.7.A	6x	nr. Arrochar, Argyll	84.0
1.6.C	6x	Oban, Argyll	87.5
21.8.B	6x	Jura, Argyll	88.0
77.8.B	6x	Inveran, Sutherland	88.0
59.7.A	6x	Lizard, Cornwall	91.0
16.8.D	6x	Connemara, Co. Galway	96.0
45.6.B	6x	Carrbridge, Inverness	108.0
53.7.N	6x	Harris, Inverness	115.25

SECTION 16 - CRITICISM OF DATA ON SEED CHARACTERS

The work on seed characters is still at a very early stage, and the results reported are only the data from preliminary observations. An insufficient number of seeds has been measured from each sample to permit an estimation of variance. Also, as the seeds were the product of open pollination in a glasshouse containing all three cytodemes, any differential effect that might be exerted by the male parent has not been taken into consideration - pentaploid seed resulting from an intercytodeme cross might be expected to be lighter than seed resulting from intracytodeme pollinations. That such intercytodeme crossing can occur spontaneously in the greenhouse is shown by the occurrence of spontaneous pentaploids as greenhouse weeds. The results do however provide a basis for further experimentation, both on the use of seed size characters to differentiate between cytodemes, and on the effect of environmental factors on seed size.

The character discussed below - testa cell lumen width - I believe to be independant of the above factors and a good qualitative character, as even poorly formed infertile seeds show the character of the female parent.

SECTION 17 - TESTA CELL LUMEN WIDTH

It has been noticed that the strongly thickened cells of the testa of some hexaploids had a very distinctive appearance which is quite different from that of most tetraploids. In the hexaploids these cells had quite a wide lumen, while those of the tetraploids are mostly very narrow and slit-like. To measure this quantatively the widest lumen diameter of a sample of testa cells was measured. In C. rotundifolia seeds there is a band of narrow cells down the straightest edge of each seed. In making the measurements this region was avoided, the cells with wider lumens occurring about the middle of the more rounded part of the seed being measured.

At first measurements were only made on one seed from each sample and only 10 cells measured (table 5.11), though several seeds from each sample were examined to see that they were similar to the one measured. Later, a further 50 cells were measured from several seeds of plants which seemed out of line with other specimens of their cytodeme (e.g. 45.6.B, and 64.8.C). This attempt to achieve better separation of the cytodemes by larger sample sizes proved unnecessary, no change in the sequence of clones classified by averages of ten testa cell lumen widths being obtained. Only the results for 10 cells are therefore given.

These results suggest that plants with testa cell lumens over 5um wide are, with rare exception, likely to be hexaploid. The only exception here is the plant from Thetford. Plants with narrower lumens may be either tetraploid or hexaploid, though most are likely to be tetraploid. It is interesting to note that the two hexaploids with the narrowest lumens are both plants which occur within the area largely occupied by tetraploids (75.7.A and 45.6.B). It seems possible that in these cases (especially the latter) the hexaploid might have been derived from surrounding tetraploids through fertilisation by an unreduced gamete.

SECTION 18 - CONCLUSIONS

The conclusions to the morphological observations described in this chapter can be divided into two sections. The first will deal with correlations between morphology and polyploid level, while the second will consider genecological differentiation.

(a) Polyploid level

It has been repeatedly concluded by those working on the subsection Heterophylla of Campanula that morphology cannot be relied upon to distinguish different closely related cytodemes (Böcher 1960 on C.rotundifolia and C.gieseckiana; Kovanda 1970b on C.moravica). The same conclusion has already

been drawn several times in this chapter when individual characters were under discussion. There is therefore no clear and absolute morphological distinction between the cytodemes. It is however possible, at least within the British Isles, to unequivocally assign a large number of plants to either the tetraploid or hexaploid cytodeme on morphological grounds alone. On the basis of morphological observations on cytologically known material it can be stated that the more delicate plants with paniculate inflorescences, thin pedicels, small (less than 20mm) trumpet shaped flowers, acute linear stem leaves, and a few transitional leaves (fig. 5.27) will generally prove to be tetraploids, while plants with stiff thick stems bearing few flowers on relatively thick pedicels, large flowers (over 25mm) or broad flowers with hemispherical corolla bases and ovaries, and blunt more or less spathulate stem leaves (figs. 5.9 and 5.24) will usually be hexaploid. This latter morphological variant had already been noticed by several plant collectors last century and described as the var. speciosa More of C.rotundifolia. All the specimens so labelled in the herbarium of the British Museum have the distinctive morphology described above and originate from the Outer Hebrides and Ireland - areas in which I have found only hexaploids. Several living naturalists have commented to me on the distinctive nature of the harebells on the Hebridean machairs and sand dunes (figs. 5.5, 5.28) so it is clear that the hexaploids of this region are rather distinct from the tetraploid form common throughout lowland Britain. Böcher (1960) compares a specimen from Slieve League, Co. Donegal, with C.dubia which Löve and Löve (1965) relate to C.groenlandica (=C.gieseckiana ssp. groenlandica). It had the few large flowers per stem characteristic of the hexaploids, though Böcher reported his plant to be tetraploid.

A most interesting discovery was that a number of different collections of herbarium specimens from the Little Ormes Head in North Wales are of the exclusively hexaploid type, and so I predict that this will prove to be another isolated site for the hexaploid cytodeme. This discovery, together with the

FIG. 5.27 Tetraploids from the Isle of Wight. On left is cultivated specimen grown from seed. The four specimens on the right are from the wild.

FIG. 5.28 Sand dune hexaploid from Harris, Outer Hebrides.

certain record of hexaploids on Ben Nevis, puts a new light on Podlech's (1965) two published records from these localities of C.gieseckiana ssp. groenlandica. It suggests that the plants Podlech examined were probably hexaploid, and that the hexaploids in general may be very close morphologically to C.gieseckiana ssp. groenlandica.

Although many British plants possess a combination of characters which enables them to be assigned to one or other of the cytodemes, there are a large number of others which cannot be so assigned. This makes it impractical to attempt to refer the two cytodemes to separate taxa.

(b) Genecology

From the discussion of individual morphological characters it is clear that British C.rotundifolia is highly variable. In fact, the differences between plants were such that, especially at flowering time, each potted plant in the greenhouse was individually recognisable. The several ramets of a cloned plant were by contrast virtually identical. The factors contributing to the distinctive appearance of an individual genotype were:-

(a) Height, habit (erect or trailing), and thickness of stem.

(b) Number, shape, colour, and disposition of leaves on the stem.

(c) Number, degree of aggregation, disposition on stem, stance (erect or nodding), shape, and colour of flowers.

These obvious characteristics, as well as less immediately obvious ones (e.g. pollen and seed characters) appeared to be correlated with a number of factors of which polyploid level was only one - the others chiefly being longitude and latitude, altitude, and habitat. The correlation of morphological characters with these four factors will now be discussed in turn.

(i) Longitude and latitude

Within the tetraploid cytodeme in the main island of Great Britain there does seem to be a general clinal variation pattern in C.rotundifolia from the south east to the north west. The pattern is little disrupted by altitudinal

variation, perhaps largely because the effects of high latitude and high altitude more or less parallel one another, and high altitude areas are found only in the north and west. Altitude does however impose another dimension on the pattern of variation. The variation observed has been seen in both herbarium specimens and cultivated material.

Topodemes from the south and east, and especially those on chalk (Cambridge, North and South Downs, Isle of Wight), tend to have paniculate inflorescences with fine branches bearing numerous small (10-15mm), often pale coloured, flowers. As one moves northwards and westwards the plants' stems become fewer flowered, more racemose, and with larger flowers (up to 25mm). Despite this general trend, small-flowered plants, in which this character is retained in cultivation, occur in the north, sometimes in otherwise large flowered populations.

Hexaploids are very rare in the southern parts of the British Isles, and so few specimens of southern origin have been seen that only very cautious attempts at generalisation can be made. In general the hexaploids are rather similar to northern and montane tetraploids, having few large flowers per stem. The only two hexaploids I have seen of really southern origin (from the Lizard and Co. Tipperary) have short rather rigid stems bearing several short but broad flowers which are held erect (fig. 5.29). In comparison to these, more northerly topodemes are mostly taller, laxer, and have often much larger (to 30mm), sometimes nodding flowers (fig. 5.28).

(ii) Altitude

Tetraploids and hexaploids vary in parallel with increasing altitude. As one ascends a British mountain (whether it be in Wales, the Lake District, Scotland or Ireland) the harebells tend to become shorter stemmed, to have blunter leaves more gathered towards the base of the stem, more and shorter transitional leaves, and fewer, larger flowers with more hemispherical ovaries (figs. 5.10, 5.24). The comparison between lowland and mountain plants is perhaps

FIG. 5.29 Cultivated specimens of a hexaploid from the Galtee Mountains, Co. Tipperary. (93.6) Specimen on left grown in warm humid greenhouse and somewhat shaded. Specimens on right from dry very light greenhouse.

best demonstrated by a comparison of figs. 5.18 and 5.28 (lowland plants) and figs. 5.10 and 5.24 (three of the most extreme mountain plants). If they were to be identified using a flora key (e.g. Podlech 1965, Kovanda 1970, Fedorov 1957), most British high mountain plants would be assigned to C. polymorpha or C. gieseckiana. In overall appearance, mountain tetraploids are closest to C. polymorpha, while the stiffer, larger flowered hexaploids with larger ovaries are closer to C. gieseckiana.

Böcher (1966), on the basis of an extensive knowledge of both subspecies of C. gieseckiana in Greenland, states that he cannot follow Podlech (l.c.) in referring some Scandinavian plants to the subspecies groenlandica of that species. From my very limited knowledge of Greenland plants I similarly believe that they are not identical with any British tetraploids, but many of the mountain hexaploids appear to be virtually inseparable from Greenland material of the subspecies groenlandica.

(iii) Habitat

It has already been remarked in the discussion of individual characters that there is much habitat correlated variation in C. rotundifolia, so only a summary of the major features will be given here.

Cliff plants, whether from maritime or mountain cliffs, are usually short, rigid, and erect, bearing flowers in tight clusters at the apex of the stems (figs. 5.8 and 5.9). Such plants, and especially those from dry maritime cliffs, often have very limited rhizome development.

C. rotundifolia plants from grassland and heath habitats have a much laxer habit, often falling over when cultivated in pots and unsupported. An almost trailing decumbent habit is sometimes found in plants from short turf in exposed situations, whether maritime (fig. 5.14) or montane (fig. 5.15c).

The habit of sand dune plants is often similar to that of plants from tall grassland. They are usually tall and vigorous with extensive rhizome

development. The most remarkable sand dune plants are the hexaploids from the extensive dune systems of Outer Hebrides and Western Ireland. Their flowers are by far the largest found in any British harebells (to over 30mm) and usually only one to four are carried on each stem. Unlike most British hexaploids their flowers are often trumpet shaped rather than campanulate. The ovaries and capsules are always very large (figs. 5.5 c d, 5.28).

The above results agree with those of Turesson (1925, 1930) who found considerable genecological differentiation in C.rotundifolia. However it is possible, and perhaps even probable, that some of his lowland specimens may have been diploid, while his high altitude and high latitude plants were probably tetraploid. He also states that one of his Alpine plants was probably referable to C.scheuchzeri, which is often considered to be quite a distinct species.

CHAPTER 6: ECOLOGY

SECTION 1 - INTRODUCTION

In this chapter I shall discuss the autecology of C.rotundifolia in the British Isles in particular drawing attention to the wide range of habitats it occupies. It was shown in the last chapter how variable this species is both genotypically and phenotypically, and how the environment can affect the phenotype. The data collected and the general methods used have been discussed in Chapter 3.

C.rotundifolia s.s. has a wide latitudinal range in Europe, from Albania in the south to north Norway in the north (Podlech 1965, Laane 1968). In the British Isles it occurs in nearly all parts of the country, from the Lizard and Kent in the south and east to Shetland and Cape Wrath in the north, and coastal west Irish situations in the west. It is recorded from all 122 Watsonian vice counties in Great Britain (Clapham et al 1962; McClintock pers.comm, - record for Orkney), and 28 of the 40 Irish vice countries (see also distribution map, fig 1.3). In many areas it occurs in a range of habitats from sea level to the summits of the highest hills. In the Central Highlands of Scotland it has been reported to ascend to 1110m (3,700ft) (McVean and Ratcliffe 1962), and I have found it up to 1140m (3,800ft) on Stob Binnein, near Crianlarich in Perthshire.

PRESENTATION OF THE RESULTS

In discussing the ecology of the species in detail I consider it best to proceed by exemplification, stating a few of the environmental parameters, but relying heavily on the list of associated species to convey an overall impression of the condition in any particular habitat. Such a technique is meaningful to most field botanists who have some idea of the range of conditions tolerated by many species, and it receives support from the work of Boyko (1947, 1949).

As mentioned in Capter 3, I at first intended to describe the associated species by means of a standard-sized quadrat. However, early on it became obvious that such an approach would be inappropriate, especially in most of the western habitats where much of the collecting was done. Here, in rock ledge communities and in crevices the environmental conditions and species groupings vary enormously over distances of a few centimeters. Consequently, description of the associated vegetation was confined to consideration of the actual turfs in which the Campanula plants were growing, wherever possible, however, some indication of the cover value of the species was given. Because of the different sizes of the turfs collected, no valid comparison could be made of the numbers of associated species in different localities. The ecology of C. rotundifolia will therefore be discussed in the following way :-

An account will be given of the major floristic associations in which it commonly occurs (Section 2) together with notes on some of the environmental parameters. This will set the background against which the range of certain environmental factors under which C. rotundifolia has been found can be discussed - these factors being

Section 3	Soil types, (including a discussion of soil texture, water-holding capacity, and moisture status in the field).
Section 4	Soil p.H.
Section 5	Degree of shading
Section 6	Shortness of growing season
Section 7	Interrelationships with animals
Section 8	Interrelationships with other plant species - parasitism and competition.

SECTION 2 - FLORISTIC ASSOCIATIONS

Floristic associations

"In dry grassy places and on fixed dunes, often in poor shallow soil", is the ecological note given in Clapham et al (1962). McVean and Ratcliffe (1962) state that though it is found on soils with a wide range of pH values it does not occur on mor humus. These accounts give some idea of the habitats in which C. rotundifolia is most conspicuous, but omit to mention another major habitat - rock ledges and crevices on maritime and mountain cliffs. It is interesting to note that in lowland habitats it is usually considered to be a species of the poorer soils (Clapham et al 1962, Gimmingham 1964, Hepburn 1952), whereas in mountain areas it is described as characteristic of the richer soils (McVean and Ratcliffe 1962, Condry 1967).

In the work described in "The Vegetation of the Scottish Highlands" McVean and Ratcliffe (l.c.) found C.rotundifolia in the communities listed in table 6.1.

Brief accounts will now be given of characteristic habitats of the three types (dry grassy habitats, dunes, rock ledges), with some of the commoner variations.

Where possible the plant communities have been described by means of data collected from a 1 metre quadrat using the domin cover-abundance scale. However in rock ledge and crevice habitats where a number of separate turfs, each containing a C.rotundifolia plant, were collected, the number of turfs in which each species was recorded is given. There are therefore two kinds of lists in the following tables; (a) those in which the cover-abundance of associated species is denoted by domin numbers, and (b) those in which the number of turfs collected is given at the beginning of the list, and the numbers following the species names denote the number of turfs in which that species was found. In this second type of list, the underlining of a

TABLE 6.1 THE FLORISTIC ASSOCIATIONS (NODA) IN WHICH C.ROTUNDIFOLIA IS REPORTED TO OCCUR IN THE SCOTTISH HIGHLANDS (McVean and Ratcliffe 1962)

NODA

Betuletum Oxaleto - Vaccinetum

Vaccinium - Luzula Treeless Facies

Fern Dominated Treeless Facies

Salix Lapponum - Luzula sylvatica nodum

Callunetum vulgaris

Arctostaphyleto - Vaccinetum

cladinosum

rhacomitrosum

Dryas - Salix reticulata nodum

Dryas - Carex rupestris nodum

Dryas - Carex flacca nodum

Species poor Agrosto - Festucetum

Alchemilleto - Agrosto - Festucetum

Rhacomitrium - rich facies

Saxifrageto - Agrosto - Festucetum

Species rich Agrosto - Festucetum

Thalictrum - Ctendium provisional nodum

Nardetum sub-alpinum

Species - rich facies of Nardetum sub-alpinum

Hypno - Caricetum alpinum

Deschampsietum cespitosae alpinum

species poor facies

species rich facies

Tall herb nodum

Cryptogrammeto - Athyrietum chionophilum

Dwarf herb nodum

Saxifragetum aizoidis

mixed saxifrage facies

Deschampsieto - Rhytidiadelphetum

typicum

triquetrosum

Molinia - Myrica nodum

species name indicates that it was a major component in the vegetation of one or more turfs - often the bryophyte species which had built up the turf.

Dry grassy habitats

Two dry grass-heathhabitats in the Eastern Highlands of Scotland are described in tables 6.2 and 6.3. The tetraploid cytodeme of C.rotundifolia is very common in such habitats throughout eastern Scotland and most parts of England. It only rarely invades the almost pure stands of Calluna which are common in the heather moors of eastern Scotland. As the hexaploid cytodeme is rare in the eastern parts of Great Britain where such dry grassy and heathy communities are frequent, it is rarely found in this type of habitat. However an example can be given from the Isle of Man (table 6.4).

In the moister climate of western Scotland really dry grassland soils are only found in special situations, as on the thin non-peaty soil covering the boulders of an old dry-stone wall (table 6.5). In general, grasslands in the west of Scotland are much wetter, and on the poorer, better drained sites in this region both tetraploid and hexaploid cytodemes may occur in heathy communities (see tables 6.6 and 6.7). The damper more fertile grasslands in the west are only occasionally colonised by the tetraploid cytodeme, the hexaploid cytodeme being even rarer in this type of habitat. The example quoted (table 6.8) is however of a hexaploid.

There are several noteworthy features about the species lists from these habitats. Festuca rubra is usually important in the communities, often in association with a species of Agrostis. The importance of bryophytes in all but two of the habitats, and even in the dry east-Highland grasslands, is also noticeable. As will be discussed in more detail in Chapter 7, this may be related to the requirements for seedling establishment.

As one ascends to higher altitudes the grasslands can rarely be described as dry, but C.rotundifolia will still be present, even in flat or only gently sloping situations, as long as the ground is well drained. The species composition of the grassland changes with altitude, Agrostis tenuis often being replaced by A.canina, and more upland species coming into the communities. Festuca rubra and Potentilla erecta however remain very constant associates of C.rotundifolia.

Towards 750m (2,500ft), C.rotundifolia is often still quite frequent in the Rhacomitrium heath communities which tend to replace grassland at these altitudes. This is too high for the proper development of blanket bog, and though the thin soils are usually cold and wet, they often overlie rock detritus or are on steep slopes and are therefore freely drained. Examples of such habitats are given in tables 6.9 and 6.10.

Another type of habitat which is perhaps best dealt with here is the machair of western Scotland and the Hebrides. This is a species rich type of community developed on low lying ground near the sea under conditions of great exposure and the influence of wind blown shell sand. The soils are therefore fertile, but the development of luxuriant vegetation is prevented by the exposure. An example of such a community containing C.rotundifolia is given in table 6.11.

Sand dunes

Most sand dune systems throughout the British Isles are probably colonised by one or other cytodeme of C.rotundifolia. Although it is sometimes considered to be more a plant of fixed dunes (Clapham et al 1962) and dune heath (Hepburn 1952) than the main dune system, it frequently occurs far forward where the sand is unstable and some accretion is taking place. Seedling establishment may be a problem in such habitats,

but turfs of almost continuously moist moss are frequently present in sheltered hollows, and once established, rhizomatous spread enables the species to colonise wide areas. Occurrences on fairly unstable sand with Ammophila present in large quantities are exemplified in tables 6.12 and 6.13 while the more stabilised situation is exemplified in table 6.4.

Rock ledges

C.rotundifolia is a frequent species on both maritime and mountain rock ledges and crevices. On highly shattered cliffs with numerous cracks its rhizomatous habit peculiarly suits it to colonising such habitats. The thin rhizome branches are able to travel a considerable distance (at least half a metre) through cracks, before re-emerging to produce leafy shoots from a crevice which may be totally unsuitable for seedling establishment. On cliffs of many rock types (particularly limestone, basalt, and mica schist) the removal of a block of rock from near a C.rotundifolia plant frequently reveals a mat of white rhizomes and roots of this species lying on the rock in the almost total absence of soil. The only other common species to behave in this way is the common associate of C.rotundifolia in Britain - Festuca rubra.

Examples of maritime cliff ledge habitats are given in tables 6.14 and 6.15 and similar mountain habitats in tables 6.16, 6.17 and 6.18. A different type of associated vegetation occurs on limestone cliffs in the Pennines and Western Ireland. An example of this type is given in table 6.19. The most important associated species are often (as in this example) Sesleria caerulea, Festuca rubra and Ctenidium molluscum, though in this western locality other bryophytes are also very abundant.

Another characteristic habitat of C.rotundifolia, somewhat intermediate between the limestone cliffs and the more calcareous grasslands, is the rocky but fairly level limestone outcrop. Such habitats occur on the

TABLE 6.2

Code No: 36.6. Locality: Struan, nr. Blair Atholl, Perthshire.

Map Ref: 27/81-65- Altitude: 180m (600ft) Habitat: Festuca-Agrostis Grassland

Soil type: Sandy Peat Soil p.H: 4.8 Soil water holding capacity: 132.3%

	Domin Nos.		Domin Nos.
Achillea millefolium	2	Ranunculus acris	2
Agrostis tenuis	9	Rumex acetosella	2
Anthoxanthum odoratum	6	Veronica chamaedrys	4
Campanula rotundifolia (4x)	2	Veronica officinalis	2
Euphrasia officinalis agg.	1		
Festuca rubra	6	Hylocomium splendens	3
Plantago lanceolata	3	Mnium undulatum	3
Pontentilla erecta	1	Rhytidiadelphus squarrosus	5

TABLE 6.3

Code No: 37.6 Locality: Struan, nr Blair Atholl, Perthshire.

Map Ref: 27/81-65- Altitude: 180m (600ft) Habitat: Heathy grassland

Soil Type: Sandy loam Soil p.H: 6.4 Soil water holding capacity: 114.7%

	Domin Nos.		
Agrostis tenuis	6	Prunella vulgaris	1
Anthoxanthum odoratum	7		
Calluna vulgaris	5	Trifolium repens	2
Campanula rotundifolia (4x)	2	Veronica officinalis	1
Festuca rubra	7	Viola riviniana	1
Nardus stricta	3		
Plantago lanceolata	2	Hylocomium splendens	7

TABLE 6.4

Code No: 101.6 Locality: The Cronk, nr. Ballaugh, Isle of Man.

Map Ref: 24/337960 Altitude: 30m (100ft) Habitat: Maritime grassland

	Domin Nos		Domin Nos
Agrostis tenuis	2	Koeleria cristata	3
Ammophila arenaria	3	Lotus corniculatus	3
Anthoxanthum odoratum	2	Luzula campestris	2
Arrhenatherum elatius	4	Ononis repens	4
Bromus mollis	2	Plantago lanceolata	3
Campanula rotundifolia (6x)	1	Poa pratensis	2
Cerastium fontanum	3	Ranunculus acris	3
Cirsium arvense	2	Senecio jacobea	2
Festuca ovina	3	Taraxacum officinalis agg.	4
Galium verum	4	Trifolium repens	4
Holcus lanatus	4	Veronica chamaedrys	3
Hypochaeris radicata	2	Viola riviniana	2

TABLE 6.5

Code No: 11.6 Locality: Lindsaig Farm, nr. Kilfinan, Cowal, Argyll.

Map Ref: 16/931795 Altitude: 60m (200ft) Habitat: Roadside grassland on thin soil overlying boulders

Soil type: Sandy loam Soil p.H: 4.75 Soil water holding capacity: 73.3%

	Domin Nos		Domin Nos
Achillea millefolium	1	Lathrus pratensis	2
Agrostis tenuis	9	Lotus corniculatus	5
Anthoxanthum odoratum	3	Plantago lanceolata	4
Arrhenatherum elatius	1	Potentilla erecta	2
Campanula rotundifolia (4x)	5	Rumex acetosa	2
Centaurea nigra	5	Succisa pratensis	1
Conopodium majus	3	Torilis japonica	1
Dactylis glomerata	4	Veronica chamaedrys	2
Epilobium montanum	1	Mnium longirostrum	1
Festuca rubra	5	Plagiothecium sp.	1
Holcus lanatus	5	Lophocolea bidentata	1

TABLE 6.6

Code No: 10.6 Locality: Ben Capuill, Tighnabruaich, Argyll.

Map Ref: 16/978756 Altitude: 390m (1300ft) Habitat: Grass heath on mica schist

Soil Type: Peat Soil p.H: 4.3 - 4.83 Soil water holding capacity: 312.9 - 389.2%

	Domin Nos.		Domin Nos.
Arostis canina	4	Polygala serpyllifolia	1
Anthoxanthum odoratum	2	Potentilla erecta	5
Calluna vulgaris	9	Vaccinium myrtillus	1
Campanula rotundifolia (4x)	4		
Festuca ovina	4	Hypnum cupressiforme	3
Galium saxatile	4	Pleurozium schreberi	1

TABLE 6.7

Code No: 28.8 Locality: Loch Carnain an Amais, nr. Tobermory, Mull, Argyll.

Map Ref: 17/468525 Altitude: 135m (450ft) Habitat: Grass Heath in Quarry

Soil type: Peaty loam Soil p.H: 4.7 - 5.35 Soil water holding capacity: 138.9 - 211.0%

	Domin Nos.		Domin Nos.
Anthoxanthum odoratum	2	Trifolium repens	2
Calluna vulgaris	6		
Campanula rotundifolia (6x)	3	Aitrichum undulatum	1
Festuca ovina	7	Hypnum cupressiforme var.	
Luzula multiflora	2	ericetorum	10
Plantago lanceolata	2	Pseudoscleropodium purum	2
Potentilla erecta	4	Rhytidiadelphus squarrosus	3
Thymus drucei	3	Cladonia cf. pyxidata	2

TABLE 6.8

Code No: 25.8 Locality: Dervaig, Mull, Argyll.

Map Ref: 17/416518 Altitude: 60m (200ft) Habitat: Roadside grassland

Soil type: Peaty loam Soil p.H: 5.5 Soil water holding capacity: 106.2%

	Domin Nos.		Domin Nos.
Achillea millefolium	2	Trifolium repens	4
Agrostis tenuis	5	Veronica chamaedrys	4
Bellis perennis	4		
Campanula rotundifolia (6x)	4	Ctenidium molluscum	2
Carex cf. binervis	2	Hylocomium splendens	5
Festuca rubra	7	Hypnum cupressiforme	4
Plantago lanceolata	4	Rhytidiadelphus squarrosus	2
Potentilla erecta	5	Plagiochila asplenioides	1
Prunella vulgaris	6	Peltigera canina	1

TABLE 6.9

Code No: 44.7 Locality: Beinn Udlaidh, Glen Orchy, Argyll.

Map Ref: 27/2--3-- Altitude: 750m (2500ft) Habitat: Rhacomitrium-Salix herbacea heath.

Soil Type: Micaceous silty peaty ranker Soil p.H: 4.3-5.8

Soil water holding capacity: 57.2 - 318.4%

	Domin Nos.		Domin Nos.
Agrostis canina	2	Salix herbacea	7
Alchemilla alpina	1	Selaginella selaginoides	1
Campanula rotundifolia (4x)	3	Thalictrum alpinum	4
Carex bigelowii	5		
Deschampsia cespitosa	2	Thymus drucei	2
Festuca vivipara	2	Rhacomitrium lanuginosum	10
Lycopodium selago	2	Cladonia uncinata	2

TABLE 6.10

Code No: 9.0 Locality: Summit plateau, Ben Alder, Inverness-shire.

Map Ref: 27/487719 Altitude: 1050m (3500ft) Habitat: Rhacomitrium heath

Soil Type: Peaty ranker Soil p.H: 4.7 Soil water holding capacity: 350.3%

	Domin Nos.		Domin Nos.
Agrostis canina	5	Deschampsia cespitosa	8
Campanula rotundifolia (6x)	5	Rhacomitrium lanuginosum	9
Carex bigelowii	5		

TABLE 6.11

Code No: 2.7 Locality: Ardlamont Point, Cowal, Argyll

Map Ref: 16/995645 - 16/989641 Altitude: 3m (10ft) Habitat: Machair

Soil type: Sandy peat Soil p.H: 6.3-7 Soil water holding capacity: 129.8 - 333.

	Domin Nos.		Domin Nos.
Achillea millefolium	5	Poa pratensis	1
Ajuga reptans	2	Ranunculus bulbosus	4
Armeria maritima	1	Thymus drucei	5
Bellis perennis	1	Trifolium repens	5
Campanula rotundifolia (4x)	4		
Carex binervis	5	Acrocladium cuspidatum	2
C.flacca	1	Dicranum scoparium	1
Centaurea nigra	1	Eurhynchium praelongum	1
Festuca rubra	6	Fissidens adianthoides	1
Hieracium pilosella	2	Hypnum cupressiforme var. tectorum	3
Lotus corniculatus	5	Mnium longirostrum	5
Luzula campestris	4	M.undulatum	5
Plantago lanceolata	5	Rhytidiadelphus squarrosus	7

TABLE 6.12

Code No: 7.7 Locality: Cheswick, Nr. Berwick, Northumberland.

Map Ref: 46/036477 Altitude: 15m (50ft) Habitat: Sand dunes

Soil type: Sand Soil p.H: 7.2-7.45 Soil water holding capacity: 24.9-32.7

	Domin Nos.
Ammophila arenaria	6
Campanula rotundifolia (4x)	4
Festuca rubra	10
Geranium molle	2
Lotus corniculatus	1
Ononis repens	3
Taraxacum officinalis agg.	2

TABLE 6.13

Code No: 76.8 Locality: An Fharaid, Balnakeil, Durness, Sutherland.

Map Ref: 29/389705 Altitude: 15m (50ft) Habitat: Sand dunes

Soil type: Shell sand Soil p.H: 8 Soil water holding capacity: 45.7-76%

	Domin Nos.
Achillea millefolium	5
Ammophila arenaria	5
Bellis perennis	4
Campanula rotundifolia (6x)	4
Dactylis glomerata	2
Festuca rubra	9
Galium verum	3
Plantago lanceolata	4
Poa pratensis	7
Ranunculus repens	2
Trifolium repens	3
Brachythecium rutabulum	2
Bryum sp.	1
Mnium undulatum	2

TABLE 6.14

Code No: 3.7, 3.8 Locality: Ardiamont, Nr. Tighnabruaich, Argyll

Map Ref: 16/985644-16/982647 Altitude: 15m (50 ft) Habitat: Maritime Cliff ledges in mica schist

Soil Type: Peaty silt Soil p.H: 4.25-6.9

Soil water holding capacity: 98.3-168.2%

12 turfs containing C.rotundifolia (4x)

	Frequency		Frequency
Aira praecox	1	Amphidium mougeottii	3
Allium vineale	1	Cratoneuron filicinum	2
Anthoxanthum odoratum	3	Eurhynchium praelongum	1
Carex flacca	1	Isothecium myosuroides	3
Centaurea nigra	1	Mnium hornum	1
Crepis capillaris	1	Conocephalum conicum	3
Dactylis glomerata	1	Saccogyna viticulosus	1
Digitalis purpurea	1	Green algal slime (Palmella)	5
Erica cinerea	1		
Festuca rubra	4		
Filipendula ulmaria	1		
Holcus lanatus	1		
Hypochaeris radicata	2		
Lotus corniculatus	1		
Pinguicula vulgaris	1		
Rumex acetosa	1		
Samolus valerandi	1		
Sedum anglicum	1		
Taraxacum officinalis	1		
Teucrium scorodonia	1		
Umbilicus rupestris	3		

TABLE 6.15

Code No: 18.7 Locality: Port Askaig, Islay, Argyll

Map Ref: 16/42-69 Altitude: 6m (20ft) Habitat: Rock ledges on maritime cliffs

Soil Type: Loam - peaty loam Soil p.H: 4.2-6.4

Soil water holding capacity: 98.1 - 204.4%

12 turfs containing C.rotundifolia (6x)

	Frequency		Frequency
Agrostis tenuis	1	Aitrichum undulatum	1
Aira praecox	3	Dicranum majus	2
Anthoxanthum odoratum	6	Fissidens taxifolius	1
Calluna vulgaris	1	Hypnum cupressiforme	4
Endymion non-scripta	1	Isothecium myosuroides	3
Erica cinerea	2	Mnium punctatum	1
Euphrasia officinalis agg.	1	Polytrichum piliferum	1
Festuca rubra	7	Weissia sp.	1
Galium saxatile	2	Saccogyna viticulosus	1
Holcus mollis	1	Cladonia sp.	1
Hyericum pulchrum	2	Parmelia omphalodes	1
Hypochaeris radicata	2	Peltigera cf. polydactyla	1
Luzula sp. (seedling)	1		
Plantago lanceolata	2		
Potentilla erecta	4		
Primula vulgaris	1		
Rumex acetosa	2		
Sagina procumbens	2		
Sedum anglicum	5		
Succisa pratensis	1		
Teucrium scorodonia	2		
Viola riviniana	1		

TABLE 6.16

Code No: 16.9 Locality: N. Coire, Cruach Ardrain, Nr. Crianlarich, Argyll

Map Ref: 27/407212 Altitude: 900m (3,000ft) Habitat: Rock ledges

Soil Type: Micaceous peaty silty rankers Soil p.H: 4.5-5.3

Soil water holding capacity: 167.7-372.4

9 turfs containing C.rotundifolia (4x)

	Frequency		Frequency
Agrostis canina	3	Polytrichum alpinum	2
Alchemilla alpina	1	Rhacomitrium lanuginosum	2
Festuca vivipara	3	Rhytidiadelphus loreus	4
Galium saxatile	3	Sphagnum plumulosum	1
Juncus bulbosus	1	Anthelia julaceae	1
Oxalis acetosella	1	Barbilophozia floerckii	2
Saxifraga oppositifolia	2	Bazzania tricrenata	1
Viola palustris	1	Diplophyllum albicans	1
		Marsupella emarginata	2
Amphidium mougeottii	1	Nardia compressa	1
Blindia acuta	1	Pellia sp.	1
Breutelia chrysocoma	1	Riccardia pinguis	1
Dicranum fuscescens	1	Cladonia cf. rangiformis	2
D. scoparium	2	Peltigera cf. rufescens	1
Heterocladium heteropterum	1		
Mnium punctatum	1		
Pleurozium schreberi	1		

TABLE 6.17

Code No: 42.7, 43.7 Locality: N. Coire, Beinn Udlaidh, Nr. Tyndrum, Argyll

Map Ref: 27/2--3-- Altitude: 690 (2,300ft) Habitat: Rock ledges

Soil Type: Micaceous silty ranker - moss peat Soil p.H: 4.2-7.8

Soil water holding capacity: 113.0-679.0%

9 turfs containing C.rotundifolia (4x)

	Frequency		Frequency
Alchemilla alpina	1	Hylocomium splendens	1
A. filicaulis	1	Hypnum cupressiforme	1
Festuca ovina	1	Mnium hornum	1
Festuca rubra	4	Trichostomum tenuirostre	1
Hymenophyllum wilsonii	1	Barbilophozia floerckii	2
Sedum rosea	1	Bazzania tricrenata	1
Selaginella selaginoides	1	Diplophyllum albicans	5
Socidago virgaurea	1	Frullania tamariscinum	1
Amphidium mougeottii	2	Mastigophora woodsii	1
Anoectangium compactum	5	Plagiochila carringtonii	1
Campylopus atrovirens	1	P. spinulosa	1
Dicranum scoparium	1	Riccardia pinguis	1
		Solenostoma sp.	3

TABLE 6.18

Code No: 16.8 Locality: N. Cliffs, Muckanaght, Connemara, Co. Galway

Map Ref: 84/7--2-- Altitude: 480m (1,600ft) Habitat: Rock ledges

Soil Type: Peat Soil p.H: 4.1-4.35 Soil water holding capacity: 182.2 - 326.7

6 turfs containing C.rotundifolia (6x)

	Frequency		Frequency
Agrostis tenuis	3	Polytrichum cf. commune	1
Deschampsia flexuosa	1	P. piliferum	1
Erica cinerea	1	Rhacomitrium lanuginosum	2
Festuca rubra	3	Diplophyllum albicans	1
Hymenophyllum wilsonii	2	Barbilophozia floerckii	1
Saxifraga spathularis	3	Frullania germana	1
Sedum rosea	1	F. tamariscinum	2
Succisa pratensis	1	Herberta straminea	2
		Lejeunea patens	1
Bryum sp.	1	Plagiochila asplenioides	1
Hylocomium splendens	1		
Hypnum cupressiforme	1		
Isothecium myosuroides	5		

TABLE 6.19

Code No: 19.8 Locality: Most westerley cliffs, Ben Bulbin, Co. Sligo

Map Ref: 95/7~~1~~ Altitude: 390m (1,300ft) Habitat: Limestone rock ledges

Soil Type: Clay ~ Moss peat Soil p.H. 4.7~7.45

Soil water holding capacity: 87.0~538.8

21 turfs containing C.rotundifolia (6x)

	Frequency		Frequency
Agrostis stolonifera	2	Hylocomium splendens	4
Alchemilla vulgaris agg.	1	Isothecium myosuroides	2
Anthoxanthum odoratum	2	Mnium undulatum	1
Carex flacca	3	Neckera crispa	3
C. pulicaris	7	Polytrichum cf. commune	1
Euphrasia officinalis agg.	1	Pseudoscleropodium purum	4
Festuca rubra	11	Rhacomitrium lanuginosum	1
F. vivipara	2	Rhytidiadelphus squarrosus	4
Helictotrichon pubescens	1	R. triquetrus	2
Hieracium sp.	1	Thamnium alopecuroides	1
Hypericum pulchrum	1	Thuidium tamariscinum	13
Linum catharticum	1	Tortella tortuosa	
Oxalis acetosella	3	Trichostomum brachydontium	2
		T. crispa	1
Saxifraga aizoides	2	Barbilophozia floerckii	1
Sesleria caerulea	14	Diplophyllum albicans	1
Thymus drucei	7	Frullania tamariscinum	3
Viola riviniana	5	Herberta straminea	1
		Lejeunea patens	1
Acrocladium cuspidatum	1	Metzgeria conjugata	1
Amphidium mougeottii	2	Plagiochila asplendides	5
Anoectangium compactum	1	P. punctata	1
Barbula sp.	2	P. spinulosa	2
Breutelia chrysocoma	5	Radula complanata	1
Bryum sp.	2	Riccardia pinguis	1
Campylium sp.	1	Scapania aspera	5
Ctenidium molluscum	13	Cladonia subcervicornis	1
Dicranum scoparium	1	Lepraria sp.	1
Ditrichum flexifolium	3	Solorina saccata	1
Eurhynchium schwartzii	1		
Fissidens adianthoides	5		

TABLE 6.20

Code No: 73.8 Locality: Borallie, Durness, Sutherland

Map Ref: 29/387653 Altitude: 30m (100ft) Habitat: Dryas heath on limestone

Soil Type: Sandy loam Soil p.H: 7.1 Soil water holding capacity: 94.0

	Domin Nos.
Antennaria dioica	2
Campanula rotundifolia (6x)	4
Carex panicea	4
Dryas octopetala	7
Festuca ovina	
Festuca rubra	7
Linum catharticum	1
Molinia caerulea	4
Selaginella selaginoides	4
Thalictrum alpinum	5
Thymus drucei	5
Breutelia *chrysocoma*	2
Ctenidium molluscum	5
Ditrichum flexicaule	4
Hypnum cupressiforme	3
Thuidium tamariscinum	1
Scapania sp.	2

TABLE 6.21

Code No: 19.7 Locality: Palmullan Burn, Nr. Straiton, Ayrshire

Map Ref: 26/374013 Altitude: 180m (600ft) Habitat: Crevices in rocks in river

Soil Type: Sandy loam Soil p.H: 6.5 Soil water holding capacity: 78.1%

6 turfs containing C.rotundifolia (4x)

	Frequency		Frequency
Euphrasia officinalis agg.	1	Rhacomitrium aciculare	3
Brachythecium plumulosum	3	R.canescens	3
Bryum bicolor	1	Scapania subalpina	1
Polytrichum piliferum	2		

TABLE 6.22

Code No: 20.8 Locality: Shores of Lough Cullin, Nr. Pontoon, Co. Mayo

Map Ref: 94/3~~~8~~~ Altitude: 30m (100ft) Habitat: Crevices in rocks on Lough shore

Soil Type: Sandy peat Soil p.H: 4.5-5.5

Soil water holding capacity: 118.0-193.3%

5 turfs containing C.rotundifolia (6x)

	Frequency		Frequency
Agrostis stolonifera	1	Barbula convoluta	2
Anthoxanthum odoratum	2	Bryum sp.	1
Calluna vulgaris	1	Ctenidium molluscum	1
Carex flacca	1	Fissidens taxifolius	1
Festuca rubra	1	Hypnum cupressiforme var. tectorum	1
F. vivipara	1	Isothecium myosuroides	1
Holcus lanatus	1	Tortella tortuosa	4
Linum catharticum	1	Trichostomum brachydontium	2
Thymus drucei	1	Cephaloziella sp.	1
Viola riviniana	1	Plagiochila asplenioides	2
		Porella laevigata	1

Pennines, the Loch Tay limestone near Blair Atholl in Perthshire, near Durness in Sutherland, and in the Burren in Co. Clare. In the latter two localities Dryas heath is the typical vegetation and details of one such community are given in table 6.20.

Related to the cliff habitats described above are the rock ledge and crevice habitats associated with streams and lakes. On cliffs it is usually exposure and lack of sufficient soil depth which prevent the development of closed woodland vegetation which would render the habitat unsuitable for the shade-intolerant C.rotundifolia. By streams and lakes it is the high winter water level associated with fast moving water or wave action which keep rocks covered by winter floods free from tall vegetation. Although such habitats are often very wet with soils almost constantly saturated (either through flushing or a high water table), they are supplied with richly aerated water which drains rapidly through the soil.

On steep sites there is rarely any barrier to the downward movement of water, while in more level situations the substrate is often river deposited sand which forms a very open soil. Examples of two such habitats are given in tables 6.21 and 6.22.

Having surveyed some of the more typical habitats of C.rotundifolia in Britain, the range of several environmental parameters will now be discussed.

SECTION 3 - SOIL TYPES (texture, water holding capacity, and moisture status in the field)

(a) Soil texture

Both cytodemes of C.rotundifolia have been found rooted in a very wide range of soil types, from coarse sands through loams to heavy clays and pure peats. The mountain soils in which C.rotundifolia plants were rooted belong to a different series, being rankers composed of usually micaceous silty rock flour with an admixture of various amounts of peat.

TABLE 6.23

CLASSIFICATION OF THE SOILS ON WHICH C.ROTUNDIFOLIA HAS BEEN FOUND IN THE BRITISH ISLES

Frequency of occurrence

Soil Type	Tetraploids	Hexaploids	Totals
Clays	9	14	23
Silts	54	13	67
Loams	36	24	60
Sands	37	52	89
Peats	60	72	132

The soils were roughly classified into clays, loams, silts, sands, peats, and moss, with various qualifying terms to denote intermediate conditions. The presence or absence of mica was also noted. Most of the silty soils and also those containing mica are mountain ranker soils. A summary of the data obtained is given in table 6.23.

Clay

The soils classified as clays were sticky when wet and became brick-like on drying. Occurrences of C.rotundifolia on clay were always in very special situations, never on fertile lowland clays. As will be discussed later, absence from fertile clays is probably the result of competition from more vigorous species. However, in cultivation on a clay soil in the relatively high rainfall area near Glasgow many plants died during thewinter, probably largely from oxygen starvation of the roots, though frost left was also an important factor with small plants.

The clay soils colonised in the wild were relatively toxic with a mineral nutrient imbalance of some sort, and always on ledges on very steep slopes allowing rapid drainage. The tetraploids on the lead-zinc mines at Tyndrum in Argyll (18.9) grew in a very heavy sticky clay which often contained crystals of galena (lead sulphide) and presumably had a high lead and zinc content. Often there was little if any associated vegetation, and extensive areas of bare soil and rock. Species occurring with C.rotundifolia included:

Agrostis canina
Asplenium viride
Sagina procumbens
Blindia acuta
Philonotis fontana
Plagiobryum zeirii
Preissia quadrata
Rhacomitrium lanuginosum
Plagiochila asplenioides
Riccardia pinguis
Solenostoma pumila

The soil appeared to be structureless and lacked the usual obvious invertebrate fauna, presumably because of its toxicity.

Tetraploids were also found on clayey soils derived from the serpentine rocks in Glendaruel (23.6), where again the general appearance of the vegetation (particularly the lack of it) and the occurrence of such species as Cardaminopsis petraea indicated the toxic nature of the soil.

C.rotundifolia has in fact been shown to be one of the species capable of evolving ecodemes tolerant of high concentrations of heavy metals (see review by Antonovics et al 1971). Judging from the habitat, Antonovics (pers.comm.) believes that the plants growing on the lead-zinc mine at Tyndrum described above are almost certainly tolerant of high levels of lead and zinc.

In North Spain the high altitude tetraploid population 30.7 grew on a calcareous clay which was white in colour and almost entirely composed of particles of calcium carbonate.

Hexaploids were found on calcareous clays on the cliffs of Ben Bulbin, Co. Sligo, in the west of Ireland. This habitat is described in table 6.19.

These soils were moist when collected and very sticky, but on drying, set to a brick-like hardness. As the Ben Bulbin cliffs are very exposed this would be likely to occur in nature, but as the plants had some roots anchored deep in the limestone rock crevices, they would be unlikely to suffer too severely from drought.

The hexaploid from the Lizard (59.7) was found on a thin clay soil overlying serpentine.

Clay soils as a whole are unfavourable to C.rotundifolia as they are rarely adequately aerated, especially in the wet British winters, and the roots and rhizomes then easily fall prey to fungi and soil micro-organisms. Also, clay soils are usually sufficiently fertile that more vigorous species will eliminate any C.rotundifolia plants that might become established. Colonisation of clays by C.rotundifolia therefore only occurs when they are adequately drained and some factor, such as the presence of toxic

amounts of mineral elements, hinders the growth of more vigorous species.

Silts

A soil is termed a silt when it is composed of very fine particles and is not sticky when wet. As mentioned above, most soils classified as silts were high altitude rankers containing varying amounts of peat. These soils were usually structureless and immature, being composed largely of rock flour, the first product formed by the action of weathering on the rocks - often mica schists. Their organic content was sometimes well decomposed peat, but more often only half decomposed fragments of moss.

The much higher frequency of tetraploids on silts is a consequence of the large number of mountain localities sampled in the Scottish Highlands. Although the hexaploid occurs on a few mountains in the Central Highlands, there are only a few mountain areas in the extreme west of Scotland (e.g. Mull) and Ireland in which it is common. Also, as a result of the wetter climate, the peat content of the soils is frequently higher than on the mainland, leading to the soils being classified in the table as peats. The greater tendancy to peat formation on the mountains in the west tends to restrict the hexaploid cytodeme to lower altitudes unless the nature of the rock (e.g. the steep basalt cliffs of Ben More, Mull) prevents blanket peat formation.

The silt soils were found under most mountain rock ledge and crevice plants, as well as the plants in mossy vegetation at higher altitudes. A typical species list from such habitats would often include such species as:

Agrostis canina
Carex bigelowii
Galium saxatile
Saxifraga stellaris
Silene acaulis
Dicranum fuscescens
Polytrichum alpinum
P.urnigerum
Rhacomitrium lanuginosum
Diplophyllum albicans
Marsupella emarginata

Such silt soils would be expected to be very poor in nitrogen and phosphorus (McVean and Ratcliffe 1962).

Loams

Loams are those soils which contain clay, silt, sand, and organic matter in such proportions that the result is a friable soil which is freely drained and not sticky like clay, yet will hold together when moist and retain water much better than a sand. Unlike the silts described above they usually have a crumb structure and are mature soils in a state of equilibrium with the vegetation they carry. Loams are often very fertile soils, in which C.rotundifolia might be expected to be eliminated by competition. However, many of the loams colonised by C.rotundifolia were on steep banks, often by streams, where erosion kept the habitat open.

The loam soils were mostly brown earths carrying a grassy vegetation. An example of one such habitat is given below:

Locality: Drum Farm, Nr. Tighnabruaich, Argyll.

Habitat: Bank at side of field.

Altitude: 120m (400ft)

Soil Description: Loam

Associated species:

Achillea ptarmica	Filipendula ulmaria	Ranunculus repens
Agrostis tenuis	Juncus acutiflorus	Rumex acetosa
Anthoxanthum odoratum	Poa trivialis	
Festuca rubra	Potentilla erecta	

Sands and Grits

These are soils which are composed of very coarse particles and are therefore freely drained. Their water holding capacity is largely determined by the quantity of organic matter present.

The sands encountered in this investigation were of two types: inland glacial sands compound almost wholly of silica, and maritime sands which usually contained a greater or lesser admixture of shell fragments. In

some cases, as in Dog's Bay in Connemara in the West of Ireland, the sand was wholly composed of shell fragments, while in the neighbouring Mannin Bay it was a pure Lithothamnion sand composed of fragments of calcareous red algae. Many of the inland sands contained varying proportions of clay and silt.

The grits consisted of larger particles than the sands, and often contained pebbles of several rock types as well as large fragments of shells.

(b) Soil water holding capacity

For the measurement of soil water-holding capacity the method described by Richards (1954) was used. Small "mono" cups were weighed, a third filled with soil and moistened with deionised water such that the soil glistened, but that there was no free water on the surface of the soil. The samples were left overnight to equilibrate and a few further drops of water added if necessary the following morning to again bring the soils to the required moisture content. The soils were then dried in an oven and reweighed, the water-holding capacity then being calculated as a percentage of the weight of dry soil.

The above method may seem very subjective and open to error, but in fact replicate samples from the same soil always gave very similar results. The moistening operation is in fact rather like a titration, and it is remarkable how much difference one or two drops of water make to the appearance of a soil around the end point.

The water-holding capacities (hereafter referred to as the W.H.C.) of the 347 soils studied are given in table 6.24. There is no major difference in pattern between the soils under the tetraploids and those under the hexaploids. Both cytodemes are commonest on soils with W.H.C.

TABLE 6.24

THE WATER HOLDING CAPACITY OF THE SOILS ON WHICH C.ROTUNDIFOLIA OCCURS

Water holding capacities of soils (percentage of dry soil weight)	F R E Q U E N C Y		
	Tetraploids	Hexaploids	Totals
19.5- 39.5	13	9	22
39.5- 59.5	25	17	42
59.5- 79.5	19	23	42
79.5- 99.5	27	17	44
99.5-119.5	19	19	38
119.5-139.5	12	16	28
139.5-159.5	5	11	16
159.5-179.5	12	10	22
179.5-199.5	10	8	18
199.5-219.5	4	8	12
219.5-239.5	3	4	7
239.5-259.5	9	3	12
259.5-279.5	7	6	13
279.5-299.5	4	2	6
299.5-319.5	6	4	10
319.5-339.5	3	3	6
339.5-359.5	1	3	4
359.5-379.5	2	1	3
379.5-399.5	2	0	2
399.5-1905	12	8	20

between 40% and 120%, though the numbers tail off only slowly with increase in water-holding capacity to 400%. C.rotundifolia is therefore most frequent on soils with relatively low W.H.C., and though both cytodemes do occur on peats with a very high W.H.C., they are much less frequent on such soils.

(c) Soil moisture status in the field

C.rotundifolia is usually considered to be a plant of dry grassy places (Clapham et.al 1962). However, observations made in the course of this study show that both cytodemes can tolerate a very wide range of soil moisture levels.

Wet habitats

The very wet habitats that are most frequently colonised are flushed rock ledges and crevices. Often, such habitats are permanently saturated with water dripping from the tussock of vegetation - sometimes an old moss tuft held in position by the roots of the harebell anchored in crevices.

In the north coire of Beinn Udlaidh (42.7 and 43.7, pH 4.2 - 7.8) C.rotundifolia (tetraploid) was almost confined to such habitats. Of 15 plants collected, 8 were growing in saturated tufts of Anoectangium compactum with other associated species being:

Agrostis tenuis	Bazzania tricrenata
Festuca rubra	Blepharostomum trichophyllum
Saxifraga oppositifolia	Leiocolea sp.
Selaginella selaginoides	Plagiochila asplenioides
Solidago virgaurea	Plectocolea sp.
Amphidium mougeottii	Riccardia pinguis
Campylopus atrovirens	Scapania undulata
Plagiobryum zeirii	

Another four grew in other wet habitats, in one case a tuft of Anthelia julacea (a liverwort which only grows in permanently saturated habitats on rock faces or submerged in pools), with Festuca rubra as the only other associated species.

In similar habitats elsewhere C.rotundifolia has been found growing in saturated tufts of Sphagnum tenellum, in one case a pure tuft (18.6.A), but in the other (6.6.A) in association with a few shoots of Agrostis canina. In other cases the wet bryophyte tufts in which the C.rotundifolia were found have been of Sphagnum recurvum (38.6.J pH 5-7.5) and Campylopus atrovirens (24.6.A).

The most unusual wet acid habitat in which a tetraploid has been found was in blanket bog on flat ground neat Crianlarich in Argyll (16.8.I pH 5.3). Associated species were :

Festuca vivipara	Sphagnum plumulosum
Juncus bulbosus	Pellia neesiana
Viola palustris	Riccardia pinguis
Breutelia chrysocoma	

However this habitat was on the bank of a stream, and so the water in the soil may well have been moving rather than stagnant and deoxygenated. Where C.rotundifolia occurs in such wet acid moorlands, it is usually confined to stream banks, probably largely for this reason. The above microhabitats are probably fairly acid, but C.rotundifolia is also found in very wet calcareous habitats as on the sea cliffs at Ardlamont in Argyll (see also Chapter 7). Here the bryophyte tussocks were of Cratoneuron filicinum (3.8.E, 3.8.F pH 6.9,), and Amphidium mougeottii (3.8.B pH 7.65, 3.8.C pH 7.0, 3.8.D pH 7.65), with Conocephalum conicum, Riccardia pinguis, and Pinguicula vulgaris as associated species.

Hexaploid plants have been found in habitats very similar to those described above for the tetraploid. In the North Coire of Ben More on Mull the hexaploid grows in habitats similar to those occupied by the tetraploid on Beinn Udlaidh. One plant (30.8.F pH 4.9) was growing in a tussock of Anthelia julacea, while another (30.8.C pH 4.6) grew in a tussock of Mylia taylori with Sphagnum recurvum as one of the associated species. One

hexaploid plant (28.8.A pH 4.7) was found growing in a bog, again on Mull. Associated species were :

Agrostis canina	Potentilla erecta
Erica cinerea	Teucrium scorodonia
Molinia caerulea	Viola riviniana
Myrica gale	

The habitat was basically a Molinia-Myrica flush, with the Molinia having a cover value of 90%. The presence of Teucrium and the large amount of Erica cinerea suggest that though the soil was waterlogged, it must have been moving and fairly well oxygenated - see Bannister (1964, 1965) on Erica cinerea.

A rather different type of wet habitat was occupied by one of the hexaploids in Glendaruel, Argyll. This plant (21.6.C pH 5.3) grew on flushed clayey soil on a river bank with the following associated species :

Ranunculus acris	Cratoneuron commutatum
Succisa pratensis	Sphagnum recurvum
Viola riviniana	Pellia epiphylla

Thus, though both tetraploids and hexaploids sometimes occupy habitats in which the soil is permanently saturated with water, these habitats are usually on cliffs or stream banks with fairly free drainage. The water is therefore moving, and presumably fairly well oxygenated in every case.

Dry Habitats

Though, at least in the British Isles, C.rotundifolia is usually thought of as a plant of dry places, there is evidence that some habitats, even in the Scottish Highlands, may be drier than the optimum conditions for the species. In south west England it is absent from coastal cliffs and grasslands which become very dry and warm towards the middle of summer, whereas on similar cliffs in other wetter cooler parts of the country it is often one of the commonest species present. As mentioned in the chapter on morphology (Chapter 5), certain morphological features characterise plants which have been droughted, and most of the plants discussed here showed such features.

The main types of dry habitats colonised by C.rotundifolia are light very sandy soils, and dry crevices in cliffs or on walls. In all such situations the Campanula's long tap root may enable it to tap deep water supplies which are often unavailable to such shallow rooted competitors as grasses. This advantage seems to help the Campanula, especially on sand dunes where the soil depth is considerable, for I have never seen drought symptoms on a Campanula on a sand dune, even though other species were wilted. However, on shallow soils overlying rock, a hard pan, or the stones of a wall, the tap root is less advantageous as all the species present have their roots matted together in the small depth of soil available. In such habitats symptoms of long-term droughting, and even occasionally wilting, have been seen in C.rotundifolia.

On sandy heath soils in the eastern Highlands of Scotland plants having the strict habit and small flowers of droughted plants are common. One plant (fig.5.18) (46.6.A) collected on a sunny roadside bank with little vegetation cover at Aviemore, Inverness-shire, grew with :

Calluna vulgaris	Erica cinerea
Deschampaia flexuosa	Polytrichum piliferum

In a heath in a similar situation a little farther south the associated species were :

Calluna vulgaris (90% cover)	Hypnum cupressiforme
Euphrasia sp.	Polytrichum piliferum
Thymus drucei	Cladonia sp.
Vaccinium myrtillus	

In many placed in the Scottish Highlands tetraploids were frequently found growing in the turf covering which sometimes develops on old stone walls. Such habitats become very dry in long summer droughts and the vegetation frequently becomes brown and parched. In all the situations examined the harebell plants remained green though signs of water deficiency were often evident. Most of the harebell roots were usually concentrated

in the thin (often only 1-2cm. deep) soil overlying the stones which was little more than a mat of grass roots. Some roots however penetrated between the stones to the well protected soil deep inside the wall which remained moist.

In one such situation (pop 41.6) near Muir of Ord in Inverness-shire the associated species were :

Agrostis tenuis	Polypodium vulgare
Deschampsia *flexuosa*	Rumex acetosa
Festuca rubra	Trifolium repens
Hypochaeris radicata	Rhytidiadelphus triquetrus

Several of the East Anglian grassland habitats also appeared to be very dry. Associated species in one such case (pop.66.8) were :

Agrostis tenuis
Holcus mollis

The tetraploid cytodeme is of course very common in sand dune habitats which might be classed as dry. However, no sign of any droughting has been noticed on sand dunes, so presumably once a seedling has become established the deep tap root penetrates to permanently moist sand.

Plants of the hexaploid cytodeme were never found in such dry habitats as could sometimes be colonised by the tetraploids. Apart from sand dune habitats in the Hebrides and the west of Ireland, the only dry situations in which hexaploids had been found are in crevices in boulders by a lough-side in Eire (pop.20.8), and on shallow soil near the coast in Cornwall (pop.59.7).

The plants in some of the boulder crevices would be subject to periodic droughts because of the small amount of soil present and the shallowness of some of the crevices. The associated species :

Agrostis stolonifera	Tortella tortuosa
Thymus drucei	Trichostomum brachydontium
Barbula convoluta	

indicate something of the conditions to which the habitat may be subjected.

The preponderance of bryophytes shows that the habitat is usually fairly moist but may become more or less totally desiccated at intervals - at least on the soil surface. (Many bryophytes can withstand desiccation of their protoplasm for a period, and the species present commonly occur on walls.) When visited, the harebell plants showed no sign of droughting.

The Cornish plant grew on a thin clay soil overlying serpentine rock. Though the site was steep and north-facing, and so shaded, the soil was very dry, and the vegetation showed signs of desiccation. The harebell plants were somewhat wilted, and no flowering stems were visible, even though it was early September.

Though the harebell in Britain is often considered to be a plant of dry soils (Clapham et al, 1962) there is evidence that it cannot tolerate much droughting.

The hexaploid cytodeme is more or less confined to northern and western areas with an oceanic climate, and high altitude sites. Thus it is only found in areas which are climatically wet and mostly rather cool. Apart from sand dunes which have already been discussed, the only really dry habitats in such a climate are where a thin soil overlies rock, and the only time a hexaploid plant was found in such a site it seemed to be suffering from drought.

The tetraploid cytodeme appears, from the habitats it occupies, to be much more drought tolerant. However this may be largely a case of drought avoidance through the possession of a deep tap root system. In droughted vegetation the harebell is frequently accompanied by such shallow rooted species as Festuca ovina, stonecrops (Sedum spp.), and Polypodium vulgare, and the harebell may only seem drought tolerant in comparison with the desiccated grass and the obviously succulent stonecrops.

Observations on plants in cultivation in pots and on wild collected material being kept in bags show that there is no resistance to desiccation. Such a resistance might be suggested by the fleshy rhizomes, and especially the somewhat swollen tap root, in comparison with such species as Polypodium vulgare and Achillea millefolium. These species frequently occur with C.rotundifolia in dry habitats and recover well from wilting. C.rotundifolia on the other hand suffers severely from wilting, being checked in its growth for several weeks afterwards, and frequently failing to recover if dehydration has progressed sufficiently far to cause the rhizomes to shrivel. Thus, unlike the Sedum species, C.rotundifolia appears to have no means of preventing serious water loss, and unlike the other species mentioned above and many bryophytes, its protoplasm lacks the capacity to survive a limited degree of dehydration.

C.rotundifolia in the British Isles therefore is able to colonise dry habitats by virtue of its deep tap rooting habit enabling it to obtain water unavailable to other species of the same community.

SECTION 4 - p.H DETERMINATIONS

Soil p.H measurements were made on samples of air-dried soil taken from the turfs in which the plants taken into cultivation were growing. Only the layer in which the Campanula roots and rhizomes were growing was sampled, as in many cases the soils were stratified and the Campanula roots were often confined to certain layers. This means that the soil samples taken were from the soil which was in immediate contact with the underground parts of the Campanula plants.

Each sample was first passed through a 2mm. mesh sieve to remove roots, twigs, and large pebbles. A small portion (1-5g) was then made into a paste in a small 'mono' cup with a quantity of de-ionised water

such that the paste was fluid but there was little or no standing water covering the soil. Most noncalcareous soils have a sufficiently high buffering capacity to make it possible to add water over wide limits, but it is clearly most satisfactory to follow a standard procedure. With soils which contain free carbonates, the addition of excess water results in an increased pH being recorded, due to hydrolysis of the carbonates (Daubenmire 1947). However, in these soils we were only dealing with calcium carbonate, and once there is free lime in a soil and the pH rises above 7, the exact pH is of little significance to plant growth (Yaalon 1957), being largely determined by the carbon dioxide concentration in the soil atmosphere.

After wetting to a paste, the samples were left to equilibrate for two hours before the pH was measured electrically using a Pye pH meter and an Ingold electrode. The values recorded are summarised in table 6.25.

The range of pH values tolerated by both cytodemes is very great. Tetraploids were found growing in soils with values from 3.65 to 8, and hexaploids from 3.8 to 8.

(a) Tetraploids

It will be noticed that the tetraploids are distributed more or less evenly over the pH range, although the numbers tail off somewhat at the higher values. To some extent this reflects the fact that many samples were collected in Scotland where highly calcareous habitats are less common than in the limestones of the Pennines and on the chalk downs.

On one very calcareous (pH 7.65) wet flush on a seaside cliff (3.8.B), presumed lime chlorosis was noticed, many of the leaves being of a sickly yellow-green colour. As plants on equally calcareous but drier, and equally wet but less calcareous, habitats did not show such chlorosis,

TABLE 6.2.5 SUMMARY OF THE pH VALUES OF THE SOILS ON WHICH C. ROTUNDIFOLIA HAS BEEN FOUND

pH value	No. of occurrences of tetraploid	No. of occurrences of hexaploid
<4.0	7	1
4.0 - 4.3	24	14
4.4 - 4.7	26	26
4.8 - 5.1	26	13
5.2 - 5.5	18	24
5.6 - 5.9	21	4
6.0 - 6.3	18	8
6.4 - 6.7	16	9
6.8 - 7.1	12	23
7.2 - 7.5	13	28
7.6 - 7.9	6	10
≥8	1	4
Totals:	188	164

it may be the combination of high pH and very wet conditions which induced the chlorosis.

The lowest pH recorded (3.65) was for peaty soil on a cliff ledge at 750m (2,500ft) on the south face of Beinn Chabhair in Argyll (7.8.A). Associated species were :

Calluna vulgaris	Diplophyllum albicans
Hypnum cupressiforme	Cladonia sylvatica
Rhacomitrium lanuginosum	

Other habitats with a low pH were found at Farleigh Common in Surrey (3.9) and on a heathy roadside near Laggan Bridge in Inverness (3.9 - 4.25).

The highest pH (8) was recorded for a limestone grassland soil from Winnatts Pass in Derbyshire, where the associated species were :

Agrostis tenuis	Poa pratensis
Bellis perennis	Porella platyphylla

No plants from this population survived long enough to make a chromosome count. As neighbouring Monksdale was inhabited by tetraploids, it seems likely that the Winnatts Pass plants were also tetraploid.

Other highly calcareous habitats occupied by tetraploids were the Aberdeen sand dunes (7.5 - 7.9), the Cronkley Fell sugar limestones in Teesdale (7.3 - 7.5), and the flushes on the seaside cliffs at Ardlamont in Argyll (6.9 - 7.65).

Less extreme pH values were obtained from heath, grassland and rock ledge habitats throughout the country.

(b) Hexaploids

Among the hexaploids there is a remarkable gap in the distribution of plants over the pH range (table 6.25), very few plants occurring in soils having a pH between 5.6 and 6.8. As hexaploids have been collected over their whole range, and much more evenly than the tetraploids, there

is unlikely to be any sampling bias. The most probable explanation is that the pH range over which the hexaploid is rare is the pH range of the more fertile British soils. That the hexaploid cytodeme is absent from such fertile soils is most likely to be a result of its poor competitive ability, which is less than that of the tetraploid cytodeme. The hexaploids thus occur primarily in two blocks, at high and low soil pH values. The high pH occurrences are shell sand habitats, as on the machairs of the Outer Hebrides (7.15 - 7.65), and limestone rock ledges as in the Burren in the West of Ireland (7.15 - 7.9), or on Colonsay in the Inner Hebrides (6.9 - 7.35). Low pH occurrences on the other hand are mostly high altitude habitats, as on Muckanaght in Connemara (4.1 - 4.5), Ben More, Mull, in Argyll (4.1 - 4.6), or the Merrick in Kircudbright (3.8 - 4.4). The lowest pH (3.8) was recorded on the Merrick in a Rhacomitrium - Salix herbacea heath. Associated species were :

Carex bigelowii	Polytrichum alpinum
Galium saxatile	Rhacomitrium lanuginosum
Salix herbacea	Cladonia sp.
Dicranum scoparium	

The highest pH (8) was recorded several times for shell sand dunes at Calgary in Mull (91.8), S.Uist in the Outer Hebrides (85.8), and Helmsdale (37.7) and Durness (76.8) in Sutherland. The associated species in this latter case were :

Achillea millefolium	Plantago lanceolata
Ammophila arenaria	Poa pratensis
Bellis perennis	Trifolium repens
Dactylis glomerata	Brachythecium rutabulum
Festuca rubra	Bryum sp.
Galium verum	Mnium undulatum

In many topodemes of both the tetraploids and hexaploids, the pH range of the soils within a single topodeme is not very great. This can be seen from the ranges found in the hexaploid topodemes described

above, the ranges being obtained from up to eleven separate samples. In a few rock ledge populations however, a very wide range of soil pH values was found within a topodeme. The actual pH values found within such topodemes are given in table 6.26

In the two sites with tetraploids, the pH of the soil on the ledges is probably largely determined by the degree of flushing. From the notes taken at the time of collection it was noticed that the wetter the soil the higher was the pH.

On the Glendaruel serpentine the site with the lowest pH, 4, was a dry rock ledge dominated by Festuca rubra. Associated species were : (dominants underlined)

Cardaminopsis petraea	Dicranum scoparium
Festuca rubra	Cladonia impexa

The site with the highest pH (6) was in the slightly flushed grassland just below the cliffs.

Associated species were :

Cerastium fontanum	Thymus drucei
Cirsium palustre	Trifolium repens
Euphrasia sp.	Viola riviniana
Festuca ovina	Aitrichum undulatum
Festuca rubra	Pleurozium schreberi
Holcus mollis	Rhytidiadelphus squarrosus
Poa pratensis	Frullania tamarisci

In the northern coire of Beinne Udlaidh C.rotundifolia was confined to the rock ledges. The plant growing in the soil with the lowest pH, 4.2, had the following associated species :

Festuca rubra	Frullania tamarisci
Hymenophyllum wilsonii	Mastigophora woodsii
Barbilophozia floerckii	Plagiochila carringtonii
Bazzania tricrenata	Plagiochila spinulosa
Diplophyllum albicans	

The plant in the soil with the highest pH (7.8) was growing in a tussock of Anoectangium compactum with a few shoots of Festuca rubra.

TABLE 6·26

Population	Serpentine cliffs Glendaruel, Argyll (4x) (22 = 26 = 61)	Beinn Udlaidh Cliffs, Tyndrum Argyll (4x) (42 = 43.7)	Durness Limestone (6x) (73-8)	Limestone cliffs, Ben Bulbin Co. Sligo (6x) (18.8)
pH values	4.0	4.2	5.45	4.7
	4.675	5.65	7.1	5.2
of	4.7	5.8		5.7
	5.1	6.1		6.5
soil	5.35	6.3		6.5
	5.625	6.4		6.65
samples	5.8	6.65		6.7
	6.0	6.85		6.85
		6.85		6.85
		7.8		6.95
				7.0
				7.0
				7.0
				7.05
				7.25
				7.35
				7.45
Range in p.H units	2	3.6	1.65	2.75

As the hexaploid sites are on limestone, the pH of the soil pockets in which the C.rotundifolia plants were growing was controlled by the balance between flushing and leaching.

At Durness the habitat was a relatively flat Dryas heath. The lower pH (5.45) was recorded for a relatively deep soil with the associated species :

Carex panicea	Solidago virgaurea
Euphrasia sp.	Viola riviniana
Festuca rubra	Acrocladium cuspidatum
Potentilla erecta	Ctenidium molluscum
Sieglingia decumbens	Hypnum cupressiforme

The higher pH (7.1) was recorded in a much less mature soil which was little more than a limestone grit with :

Festuca rubra
Thymus drucei

On Ben Bulbin C.rotundifolia grew on small pockets of a very sticky clay soil obviously derived by solution from the limestone. It was very surprising to find that a small quantity of soil on a limestone ledge could have a pH as low as 4.7. On this ledge a large C.rotundifolia plant (rooted in the soil and only to a limited extent having contact with the underlying rock) grew in a mat of Isothecium myosuroides. The associated species were :

Festuca rubra	Diplophyllum albicans
Isothecium myosuroides	Frullania tamarisci
Rhacomitrium lanuginosum	Plagiochila spinulosa

The associated species on the ledge with the highest pH (7.45) were :

Anthoxanthum odoratum	Breutelia chrysocoma
Carex pulicaris	Ctenidium molluscum
Euphrasia sp.	Hylocomium splendens
Festuca rubra	Rhytidiadelphum squarrosus
Linum catharticum	Thuidium tamariscinum
Poa pratensis	Trichostomum brachydontium
Thymus drucei	Riccardia pinguis
Viola riviniana	Scapania aspera

An interesting observation was that the soil samples taken from the habitat of one of the pentaploids on Ben Lawers had a much higher pH (7.2) than the soils in which the tetraploids were growing (3.9 - 5.5----5 samples). The other pentaploid grew in a mat of Rhacomitriam lanuginosum with roots in rock crevices and there was insufficient soil to sample. There was no obvious difference in the species associated with the pentaploids and those associated with the tetraploids. The first mentioned pentaploid was growing through a tussock of Cherleria sedoides, but so was one of the tetraploids, and in this latter case the pH recorded was 4.4.

SECTION 5 - DEGREE OF SHADING

C.rotundifolia is usually considered to be a plant requiring full sun and my observations confirm this as a general rule. In Britain it is characteristically a plant of grassy and heathy communities and is rarely found in woodland. In such habitats it usually flowers freely. Considering the number of flowers produced, the amount of vegetation visible at flowering time is very small. For example, two stems, each bearing several flowers, might be accompanied by 1-3 vegetative shoots bearing only 1-2 leaves each (see also Chapter 7).

In cliff, and more particularly gorge, rock ledge and crevice habitats, C.rotundifolia plants are often subject to varying degrees of shading. This has a very marked effect on the morphology of the plants (see Chapter 5), there being many more leaves, especially rotund basal ones, produced in proportion to the number of flowers. The stem leaves are also broader, and each stem carries a much reduced number of flowers - often only one (fig.5.29).

Harebells in woodlands show the same morphological trends with reduced light intensity as those described above. Thus, though in the

British Isles it is not a woodland species, C.rotundifolia does show the increase in leaf area with reduced light intensity characteristic of woodland plants (but also shown to some extent by sun plants).

Although no physiological experiments have been carried out, and the dangers of misinterpreting subjective observations are realised, it is predicted that the photosynthetic efficiency of C.rotundifolia in strong light is high. A large crop of flowers and seeds, and considerable rhizome development often seem to be supported by a remarkably small leaf area.

Tetraploids and hexaploids behave similarly in response to reduced light intensity, so the above comments apply equally to both cytodemes.

SECTION 6 - SHORTNESS OF GROWING SEASON

The observations of Mathon (1959) have shown that C.rotundifolia is a long-day plant, requiring a photoperiod of over nine hours before it will flower. However, other physiological factors are also involved in the control of leaf shape, stem internode elongation, and also of flowering itself. For instance, Icelandic genotypes appear to require a fairly protracted period at a relatively lower temperature (5-6 weeks at 15°C) before the production of truly linear stem leaves, stem internode elongation, and flowering will occur. Podlech (1965) quotes Goebel as stating that the rotund, basal type of leaf is formed under condition of low light intensity, but this cannot be the only factor involved as such leaves are often produced in rosettes in the axils of linear stem leaves following decapitation of the stems. All genotypes collected in the British Isles will flower more or less continuously in a warm greenhouse (c20-25°C) with continuous light or an 18 hour day. This trait is most useful in crossing experiments, but growing a plant under such conditions for long periods may seriously weaken it. No flowering occurred in short days.

The pattern of these responses suggests that a physiological investigation of the factors controlling the various morphological developments leading to flowering would ~~repay investigation~~ study, be worth while. Also, the behaviour of the Icelandic genotypes indicate genotypic variation within the complex in such physiological requirements. All the events leading to flowering have to occur between the winter and the following flowering season. There is no pre-induction or laying down of flower buds in the previous autumn. Thus the time of flowering will be controlled by the rate of development in each season after the first occurrence of days of a certain length. In cultivation in a heated but unlit glasshouse, flowering has been noticed as early as the beginning of May, so it can be presumed that in the wild, development is slowed by low temperatures. On the continent, flowering may begin in late May, but in the British Isles it is usually much later. The first flowers rarely appear before mid-July in Scotland, and may be later following a cold spring such as that experienced in 1972.

Above 600m (2,000ft) in the mountains of the Scottish Highlands anthesis is frequently delayed till mid-August, even in a good year. One of the Ben Lawers pentaploids at about 1100m (3,700ft) was in bud on 24th August 1969. As the first snows and the end of the growing season usually arrive sometime in September, only in favourable situations in favourable years will such plants produce seed.

However, despite the fact that plants at moderately high altitude rarely produce seed, C.rotundifolia is frequently found in very high altitude sites in which seed production must be impossible under present climatic conditions. Long distance seed dispersal is one possible explanation of such occurrences, but the arguments presented in Chapter 7

suggest that this is not likely. That in some instances the high altitude plants are hexaploid while those at lower altitudes on the same mountain are tetraploid also argues in favour of the high altitude plants, whether tetraploid or hexaploid, being relicts of a period when the climate was warmer.

The highest altitude at which a C.rotundifolia plant has been collected is 1040m (3,800ft) on Stob Binnein, Near Crianlarich, Argyll. It was tetraploid and grew in a rock crevice just below the summit in association with Polytrichum alpinum and Diplophyllum albicans.

The population with the shortest growing season was probably that found at 900m (3,000ft) on Cruach Ardrain, which on 10th June 1969 had just emerged from a snowdrift. The rhizomes were just beginning to produce their first small rosette leaves - a developmental stage usually attained by lowland plants in the same area in March. The general appearance of the habitat, and the associated species :

Galium saxatile	Anthelia julaceae
Dicranum fuscescens	Marsupella emarginata
Mnium punctatum	Nardia compressa

made it clear that this was a regular late snow patch - a very unusual habitat for C.rotundifolia.

Weak, often non-flowering plants were frequently found in obviously cold damp habitats high in the mountains. These were commonly deep shady cracks in cliffs in north to north-east facing crags. The hexaploids on Ben an Lochain (1.1.A) and Aonach Beag, Nevis range (29.A) were in such situations.

Tetraploids were found in similar situations on several mountains : Cruach Ardrain near Crianlarich; Beinn Dorain near Bridge of Orchy; and Ben Narnain near Arrochar, all the sites being in Argyll. Associated

species included :

Saxifraga oppositifolia	Anastrepta orcadensis
S. nivalis	Anthelia julacea
S. stellaris	Nardia compressa
Polytrichum alpinum	

indicating the coldness of the habitat, for only under such conditions do these arctic-alpines survive in the British Isles today.

SECTION 7 - INTERRELATIONSHIPS WITH ANIMALS

There is very little further information to add to that already given in Chapter 2 on the pests of cultivation. Perhaps the only comment which should be added here is that the Sciara grubs, which were such a menace to plants in cultivation, have been found in association with C.rotundifolia roots and rhizomes in the wild. If plants collected in the wild are kept too moist in polythene bags for too long a period they are frequently attacked by the grubs in the same way as overwatered pot plants.

The gall insect Perissa tachelii Wachtl. has never been found on cultivated plants, and so is presumably incapable of surviving and completing its life cycle under the conditions in which the plants are cultivated. The presence of such galls does not seem to have any marked effect on the plants, but obviously must weaken them to some extent.

No sign of any caterpillar or other herbivore selectively attacking C.rotundifolia has been noticed. Cattle, however, certainly eat C.rotundifolia in their relatively unselective grazing.

SECTION 8 - INTERRELATIONSHIPS WITH OTHER PLANT SPECIES

Parasites

Both tetraploids and hexaploids have been found infested with the rust fungus Coleosporium campanulae Lev. No investigations were carried out on the cross-infectivity of the strains found on the two cytodemes.

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As in the case of the gall insect, the rust had no conspicuous effect on the vigour of an infected plant.

Competition

As would be expected of a common species, C.rotundifolia has been found growing in association with a large number of species (at least 150) of the vascular plants found in the British Isles. As most of the populations sampled were in Scotland, and in particular in the Highlands, the following comments apply to those areas in particular. However, observations on populations throughout the British Isles suggest that they are probably valid over a much wider area.

There are two types of common species with which C.rotundifolia does not occur. Firstly annual weeds such as Senecio vulgaris, Stellaria media and Poa annua which are typical of fairly fertile ground which is regularly disturbed. Secondly the major agricultural grasses such as Lolium perenne, Phleum pratense, and Alopecurus pratensis which are typical of fertile soils and respond vigorously to fertiliser. This avoidance of the communities on the more fertile soils, particularly by the hexaploid, seems to be the result of an inability to compete with the other species in such communities. In cultivation in pots or in the garden, C.rotundifolia shows no aversion to fertile soils, in fact it grows more vigorously than it does on less fertile soils. However, its response to increase in fertility is less than that of native species of fertile soils, and very thorough weeding must be carried out if C.rotundifolia plants are to survive in these soils. C.rotundifolia is therefore a species of low competitive ability on the more fertile soils of the British Isles.

Although the seedling can develop to maturity within one growing season (at least in cultivation), and a single capsule can yield a large

number of seeds, C.rotundifolia is not a weed species. On more fertile soils (e.g. experimental gardens) any seedlings which begin to develop are soon swamped by the more vigorous annual weeds already mentioned. On less fertile disturbed soils (e.g. rubble piles, mining detritus, and disturbed sand dunes) on the other hand, C. rotundifolia, and even the hexaploid cytodeme, may be one of the chief colonising 'weed' species. The associated species may include depauperate specimens of the annuals mentioned above and such perennials as Bellis perennis and Plantago lanceolata.

Mention will be made (Chapter 7) of the apparent superior competitive ability of young plants.

Relatively slow development and low competitive ability therefore determine the relationship between C.rotundifolia and other plant species.

SECTION 9 - CONCLUSIONS

From a consideration of the principal habitat types occupied by C.rotundifolia and the range of variation tolerated in certain environmental factors a number of useful generalisations may be made about the ecological requirements of C.rotundifolia in the British Isles.

(a) It usually occurs in habitats with a high light intensity and little or no shading. All the habitats on fairly level ground have short grassy vegetation or, if the vegetation is tall, as on sand dunes, relatively open conditions with much bare soil. In this country C.rotundifolia is rare in woodland vegetation, although in Iceland it is a conspicuous constituent of the birch woods in which the dominant species of the field layer is Agrostis tenuis. When shady habitats are colonised in gorges there is rarely much pressure of competition from other species.

(b) The soils on which C.rotundifolia occurs are probably fairly well oxygenated, being either dry, or if wet, having good drainage. The soils themselves are usually of an open character, either sandy or peaty. If it is found on heavy and sticky soils then normally these are very well drained.

(c) Generally C.rotundifolia occurs on relatively infertile soils and it therefore rarely occurs with species typical of the fertile lowland clay and loam soils. However occasionally it does occur on fertile soils as on cliff ledges, but only where exposure and the lack of soil depth prevent the proper development of vigorous species.

(d) From the study of the pH range of the soils colonised by C.rotundifolia it can be seen that both cytodemes are able to tolerate a very wide range; 3.65 to 8 in the case of the tetraploids and 3.8 to 8 for the hexaploids. This agreed with the conclusion reached by McVean and Ratcliffe (1962) in their study of Scottish Highland vegetation (though of course they did not distinguish between tetraploids and hexaploids). Future experiments will demonstrate whether ecodemes adapted to different levels of soil pH have evolved. Work on other species (e.g. on Teucrium scorodonia by Hutchinson 1967 a and b; Euphorbia thymifolia by Ramakrishnan 1961, 1965 a and b, 1966; Cynodon dactylon by Ramakrishnan and Singh 1966; and Trifolium repens by Snaydon 1962) would lead one to expect that such ecodemes would be found.

CHAPTER 7: REPRODUCTION AND POPULATION STRUCTURE

SECTION 1 - INTRODUCTION

The two previous chapters have dealt with the variation in morphological form of the mature plants and the habitats occupied by *Campanuiz rotundifolia*. However, nothing has yet been said of the way in which mature plants develop from seeds, or of the way in which a seedling becomes established, and under what conditions. These considerations are the subject of this chapter.

The chapter will begin with a discussion of the pollination mechanism and breeding system. This will be followed by a section on seed dispersal, which leads into a consideration of germination, the morphological development from the seedling stage, and the occurrence of seedlings in the wild. In conclusion, the relevance of the information obtained from the above observations to the structure and genecology of topodemes of *C.rotundifolia* will be considered.

SECTION 2 - POLLINATION

The flower structure and mode of development of *C.rotundifolia* is similar to that most frequently found in the families Campanulaceae and Compositae. Within the genus Campanula this has been described by Knuth (1909). The details of flower development and pollination in *C.americana* have been dealt with by Barnes (1885), and the precise mechanism in *C.rotundifolia* appears from observation to be identical.

In the flower bud the anthers are appressed to the style which bears numerous hairs. Before the bud opens the anthers dehisce and shed their pollen on to these stylar hairs. As the bud opens the anthers wither and the style with attached pollen is exposed. The stigmatic surface is still completely protected at this stage (figs.5.21, 5.25). In a flower in this condition nectar is secreted by the nectaries on top of the ovary, and a

bee probing for this between the expanded fringed bases of the filaments would be likely to collect pollen on its back by rubbing against the stylar hairs.

As the flower ages the stylar hairs invaginate like the finger of a glove if the wearer removes his finger but pulls the glove finger back towards the palm of his hand. The pollen is therefore no longer held by the hairs and in the wild is removed by the action of wind and rain. In cultivation in a greenhouse the somewhat sticky pollen remains on the style, but the slightest touch usually causes much of it to fall off.

At about this time the three lobes of the stigmatic surface become exposed as the three arms, which have previously been appressed, begin to curl backwards from the tip of the style (fig.5.22). At first the lobes are patent, the stigmatic surfaces facing the mouth of the flower, but later they become recurved and may touch the style. Once the stigmatic surfaces are exposed a visiting bee would first come in contact with this before it touched any pollen that might remain on the style. Once the stigma lobes have recurved pollen could fall on to them from the style, and by curling back to touch the style they might come into direct contact with the pollen. However, in the wild, and frequently even under glass, all the pollen has usually dispersed before the stigmatic lobes become recurved.

It has often been suggested on mechanistic grounds (Knuth 1909, Clapham et al.1962) that if cross pollination does not occur, then the recurving of the stigma's lobes self-pollinates the flower, and this has been confirmed by Block (1964). It has even been suggested that fertilisation may occur through the stylar hairs. Gadella (1964) could find no evidence that either of these processes, which were put forward purely on the basis of the structure of the flower, lead to fertilisation.

According to Knuth (l.c.) a wide range of insects including Coleoptera, Diptera, Hymenoptera and Lepidoptera, visit the flowers of C.rotundifolia. Bees however are the most prominent visitors (Knuth l.c.) as might be expected of a large blue flower with a structure such as that found in C.rotundifolia. In fact the only insects I have observed to visit the flowers are humble bees of an unidentified species. Very few visits have been observed, but a flower remains open for several days, and in plants visited later in the season most capsules have enlarged and contain seed. The majority of flowers must therefore be cross-pollinated for, as will be shown later, most plants are totally self-incompatible.

SECTION 3 - BREEDING SYSTEM

Most of those who have worked on the breeding system of C.rotundifolia have come to the conlusion that all three cytodemes are most probably totally self-sterile (Gadella 1964, Block 1964, Kovanda 1970a). Block (l.c.) obtained some seed as a result of the self pollination of a plant from Glen Coe - probably a tetraploid. However she could not rule out the possibility of contamination with foreign pollen. She has however shown that in one hybrid plant selfing could yield seed at the beginning of the flowering season but fail later on in the year. There have been many recorded instances of self-compatible polyploids being related to self-incompatible diploids (Fryxell 1957). Chromosome doubling using colchicine (Stout and Chandler 1941) may result in self-compatibility in the tetraploid whereas the diploid was self-incompatible. This is interpreted as the result of the duplication of the incompatibility genes.

The results obtained by Bielawska (1964, 1968) are in total contrast to those described above. She reported that all Polish tetraploids examined were somewhat self-compatible, in certain cases highly so.

In the course of the work for this thesis a study has been made of the breeding system of several diploid, tetraploid and hexaploid plants.

Experimental methods

Artificial pollinations were made by removing pollen from the style of the male parent with a dissecting needle and applying it to the stigmatic surface of an emasculated flower of the female parent. The success rate, as judged by the number of capsules setting seed relative to the number of flowers pollinated, was well over 50% in compatible crosses. For crosses within each cytodeme between plants collected within the British Isles the success rate was 60.7% (85 out of 140 pollinations) for the tetraploids, and 77.1% (27 out of 35 pollinations) for the hexaploids. On the 26 crosses made between tetraploids 22 yielded some capsules with seed, and of the 9 between hexaploids all 9 yielded at least one capsule with seed.

The greater success obtained with the hexaploid is almost certainly in part a result of the larger size of all parts of most hexaploid flowers which renders them easier to handle and less easily damaged.

Once flowers had been pollinated they were protected from contamination by being enclosed in small packets made from cellophane, greased paper, and 'sellotape' held in position and closed by paper-clips (fig.5.1). A major problem encountered with some crosses was that the sheltered conditions inside these bags provided an ideal habitat for the red spider mite. These sometimes attacked the green developing capsules to such an extent that they became almost colourless, in which case the cross usually failed. If discovered in time such infections were dealt with in several ways :- (a) by killing and removing the mites by rubbing with the fingers (this destroyed both adults and eggs but rarely removed them all); (c) by washing the capsules with a jet of water (removing most adults and some eggs but doing less damage to the capsules than rubbing); (c) by spraying a little malathione aerosol into the bag. Such infection and treatment always caused greater

damage to the smaller more delicate tetraploid capsules than the larger more robust capsules of the hexaploids. The best method of avoiding trouble from the red spider mite was to remove the bags as soon as possible after the stigmas and styles had withered and to spray frequently with water.

It is well known (Fryxell 1967) that pollinations made before the stigma would normally be receptive are sometimes successful where natural pollinations made later would fail. In C.rotundifolia I occasionally used this forced pollination technique for pollinations that had previously failed to yield seed when carried out on mature stigmas. The method used was to move apart the appressed lobes of the stigma of a young flower and apply pollen to the stigmatic surface. No viable seed was obtained by this method in pollinations that had earlier proved incompatible, though thin shrunken seeds in fully formed capsules were produced from crosses which had formerly failed totally.

Another factor which may affect the success of a pollination is the temperature under which the plants are grown. It has been shown (Fryxell 1967) that as the temperature rises compatible pollen tubes grow more quickly but incompatible pollen tubes grow more slowly. Differences in temperature could therefore determine whether a particular pollination will be successful or not. Most of the pollinations carried out in this study were performed in greenhouses in which the temperature would usually be above that expected in the wild.

As the seed capsules of C.rotundifolia are inverted and open by basal valves, the seeds will not fail out of an undisturbed capsule even if it is dry and has dehisced. However, the seed ripens and turns purple while the capsule is still a greenish colour, and it usually takes several days for it to turn yellow-brown and become dry. It is therefore possible to collect every seed produced.

Despite the problems discussed above, C.rotundifolia has a flower which is easy to emasculate and pollinate. Also, as a successful pollination can result in the production of 100 to 200 seeds (the usual contents of a single capsule), it is not too difficult to obtain large progenies.

The results obtained from self-pollinations in this study are presented in tables 7.1 and 7.2.

Tetraploids

Of the 15 tetraploid plants selfed it was interesting to discover that two set a few viable seed. Plant 65.6.E produced a few viable seed in each capsule with an average of 8 per capsule. The germination of the few seed formed was good - 90.6%. Plant 77.7.A on the other hand produced capsules containing seed in which development had been arrested at many stages of development e.g. a single capsule often contained a complete range of structures from dried ovules, through shrunken seeds of all sizes, to fully formed seeds. It was therefore very difficult to assess the number of seeds formed in each capsule. For 10 capsules the average was about 16.3 seeds per capsule with an average of 0.9 seeds per capsule appearing to be fully formed and probably viable. Of a large number of seeds sown 24 germinated.

In the case of these two plants a few self pollinations carried out early in the programme yielded a very few seeds per capsule. To rule out any possibility of this result having been obtained through contamination the plants were isolated, several inflorescences carefully bagged, and sealed. Thus a large number of flowers were isolated in a bag which came to contain a large amount of loose pollen which it was hoped would reach some of the receptive stigmas simply as a result of shaking the bag. As the majority of capsules produced a few seeds each, it is considered that these were most likely to have been produced as a result of self-fertilisation. (If one or two capsules had each produced a lot of seed and the rest had been totally

TABLE 7.1

THE RESULTS OF SELF-POLLINATING TETRAPLOIDS FROM THE BRITISH ISLES

Code No. of plant	Locality	Capsules +seed	Capsules -seed	Seed Average No. per capsule	Percentage germination
41.6.A	Muir of Ord, Ross and Cromarty	0	9	0	0
41.6.B	Muir of Ord, Ross and Cromarty	0	14	0	0
41.6.C	Muir of Ord, Ross and Cromarty	0	15	0	0
69.8.A	Moy, Inverness	0	5	0	0
45.6.A	Carrbridge, Inverness	0	31	0	0
46.6.A	Aviemore, Inverness	0	6	0	0
46.6.F	" "	0	∞	0	0
49.6.H	Dalnaspidal, "	2	∞	Infertile	0
38.6.F	Blair Atholl, Perthshire	2	40	Infertile	0
38.6.I	Blair Atholl, Perthshire	4	∞	Infertile	0
77.7.A	Bridge of Orchy, Argyll	68	∞	0.9	$\frac{24}{\infty}$
88.6.A	Ben Lui, Perthshire	0	2	0	0
28.6.A	Ben Ime, Nr. Arrochar, Argyll	0	∞	0	0
89.6.C	Ben Ime, Nr. Arrochar, Argyll	0	4	0	0
64.6.B	Campsies, Stirling	0	52	0	0
65.6.B	Cramond, Nr. Edinburgh	12	∞	8	90.6 $(\frac{87}{96})$
10.6.A	Tichnabruaich, Argyll	0	2	0	0
51.6.B	Girvan, Ayrshire	0	8	0	0

sterile, contamination would then have been the more probable explanation - c.f. Block 1964). This technique gave positive results with the two plants which were suspected of being slightly self-compatible, and also reinforced the negative results which had been obtained with other genotypes.

The habitats in which these two self-compatible genotypes were collected are of some significance. Plant 65.6.E was collected on Cramond Island in the Firth of Forth, and 77.7.A at 1050m (3,500ft) on the summit of Beinn Dorain in Argyll. Both localities are situations in which self-compatibility could be of selective advantage. On an island a colonising totally self-incompatible individual would be unable to reproduce by seed, whereas a self-compatible individual would produce at least some seed (Arasu 1968). In arctic areas self-compatible topodemes have been evolved in some species which are self-incompatible further south (Baker 1948). For much the same reasons (isolation of individuals, lack of pollinating insects) self-compatibility might be expected tobe of advantage in montane habitats.

In spite of these instances of self-compatibility, it appears from the data that many tetraploid C.rotundifolia topodemes are totally self-incompatible. Every effort was made to obtain selfed seed from the white flowered plant 64.6.B. Fifty two flowers were individually self-pollinated, thirteen of them by forcing apart the stigmatic lobes before they would naturally be exposed. No seed was obtained.

From the above results I believe I have conclusively shown that self-compatible tetraploid genotypes of C.rotundifolia exist in certain localities. It would be most instructive in future work to examine the self-compatibility of plants from a range of habitats, particularly those isolated ones in which self-compatibility could be considered of selective advantage.

TABLE 7.2

THE RESULTS OF SELF-POLLINATING HEXAPLOIDS

FROM THE BRITISH ISLES

Code No. of Plant	Locality	Capsules +seed	Capsules -seed	Seed Average No. per capsule	Percentage germination
76.8.C	Durness, Sutherland	1	2	6	33 ($\frac{2}{6}$)
45.6.B	Carrbridge, Inverness	2	4	12	54 ($\frac{19}{24}$)
61.6.E	Strontian, Inverness	0	2	0	0
31.8.A	Mull, Argyll	10	∞	8.6	29
22.8.G	" "	0	∞	0	0
1.6.A	Oban, Argyll	0	18	0	0
2.6.A	" "	0	3	0	0
75.7.A	Nr. Arrochar, Argyll	0	1	0	0
1.1.A	" "	10	0	7.1	21
83.8.D	Widdybank Fell, Upper Teesdale	3	3	Few	61.5
101.6.G	Isle of Man	0	8	0	0
20.8.c	Pontoon, Co. Mayo	0	1	0	0
16.8.A	Muckanaght, Connemara	0	3	0	0
93.6.A	Galty Mts, Co. Tipperary	1	13	9	75 ($\frac{6}{9}$)
92.6.A	Lizard, Cornwall	36	∞	Few	88.3

Hexaploids

The only published report of self-pollination experiments in hexaploid C.rotundifolia is that of Gadella (1964). He selfed a total of sixteen flowers on two plants, neither plant produced seeds.

The results of my own studies are presented in table 7.2. Seven of the thirteen genotypes tested proved to be somewhat self-compatible. As in the case of the tetraploids, only a few seeds were produced in each capsule, but in many cases (e.g. plant 1.71.A) almost every capsule contained seed. It thus seems that many hexaploids possess a limited degree of self-compatibility.

In the only case in which a mature plant was grown from a seed resulting from selfing (plant 93.6.A), the single surviving plant from the six seedlings was small and weak. It also had anomalies in its floral structure (fig.7.1), having fewer than the normal number of parts in each whorl, and structures which were half sepal-half petal, and half petal-half stamen. Plants with such anomalous flower structures have not been noticed in the wild. If weakness and anomalies of this type are confirmed in the progenies from other self-pollinations it would seem that although self-fertilisation may be possible, its products may be at a selective disadvantage, seeds from cross pollination having a greater genetic future.

SECTION 4 - SEED PRODUCTION

Campanula rotundifolia regularly produces large quantities of viable seed in the wild. The seed probably ripens between mid-August and early October. Observations in localities throughout Britain suggest that most of the seed has been scattered and the capsules reduced to skeletons of veins by early December (table 7.1).

The small number of samples and the fact that climatic conditions vary from year to year make it impossible to make any definite statement about seed maturity date and latitude. It seems possible that seed matures earlier

TABLE 7.3 OBSERVATIONS ON SEED PRODUCTION IN THE WILD - DETAILS OF LOCALITIES IN WHICH SEED WAS FOUND, IN SEASONAL CHRONOLOGICAL ORDER.

1) 19.8.1968 (52/87-86) (64.8) Firebreak in forestry plantation, Thetford Chase, Norfolk. A few dry ripe, and many green capsules.

2) 24.8.1967 (08/981919) (53.7) Sand dunes, Northton, S. Harris, Outer Hebrides. Fully formed green capsules with mature, but unripe seed.

3) 2.9.1967 (53/827223) (70.7) Sandstone common near Fakenam, Norfolk. Ripe seed present.

4) 4.9.1968 (38/95-11-) (84.8) Sand dunes, Aberdeen. Ripe seed present.

5) 5.9.1970 (36/274728) (13.0) Rock ledge, Arthur's Seat, Edinburgh. Dry ripe and green capsules present.

6) 12.9.1966 (44/649615) (79.6) Calluna heath, Strensall, Yorkshire. Ripe seed present.

7) 16.9.1967 (52/55-55-) (65.7) Chalk grassland, Fleam Dyke, Cambridgeshire. Ripe seed present.

8) 16.9.1970 (35/859384) (15.0) 360m (1200ft) Pasture, Ireshopeburn, Weardale, Co. Durham. Most stems bore one or two ripe capsules with open pores (but with most of the seed still remaining within the capsule) and several unripe green capsules. Many stems still bore flowers.

9) 26.10.1967 (27/266056) (72.7) 600m (2000ft) Mountain rock ledge, Ben Arthur, Arrochar, Argyll. Capsule skeletons present, all seed shed. All stems dry.

10) 5.12.1969 (17/834281) Grassland on seaside cliffs. Oban, Argyll. Capsule reduced to skeleton of veins except for membrane across top of capsule to which some seeds were stuck. All stems dry.

11) 5.12.1969 (17/742176) Very exposed seaside cliff, Easdale near Oban, Argyll. Capsule reduced to skeleton of veins. No seed present. All stems dry.

12) 6.12.1969 (26/883414) (45.9) Very sheltered position under overhang in river gorge, Falls of Clyde, Lanark. Seed still present in intact capsules with open pores. All stems dry.

13) 14.12.1967 (27/318303) (79.7) 300m (1000ft) Mountain rock ledges in gully, Tyndrum Argyll. Some seed present in tattered capsules.

FIG. 7.10 Abnormal flowers on offspring from the self-pollination of plant 92.6 from the Lizard, Cornwall.

in southern England than in north Scotland. Further extensive field work and experiments would have to be carried out before any general pattern of seed maturity date could be established.

At altitudes of over 600m (2,000ft) ripe seed is probably regularly produced each year, the skeletons of fully formed capsules having been found at 600m (2,000ft) near Arrochar in Argyll, and seedlings seen at 675m (2,250ft) on Bed Alder (see below) in the central highlands. At higher altitudes seed may not be produced every year, and it is possible that in some extreme situations C.rotundifolia may have perennated vegetatively for many years, the growing season being too short for the maturation and ripening of seed. For example, on August 2nd, 1970 at 1050m (3,500ft) on Ben Alder only small buds (2 mmlong) were present on an extensive (1 m sq.) but isolated colony in Rhacomitrum heath (table 6.10). On the 20th of August 1969 at 900m (3,000ft) on a rock ledge above a snow patch, in the N.E. coire of Aonach Beag, Nevis range, an isolated plant bore a single flower and a bud, while at 1110m (3,700ft) on Ben Lawers on the 24th August 1968, several plants bore swollen buds. In the seasons in which those three plants were observed it is doubtful if they could have produced mature seed before the growing season came to an end. However one plant in the Ben Lawers population bore old stems with the remains of capsule skeletons, which looked as if the capsules might have produced seed the previous year.

SECTION 5 - SEED DISPERSAL

The fruit of C.rotundifolia is a capsule containing many (up to 300) seeds. The pedicel bends over after flowering so that the capsule is inverted at maturity and opens by three valves at its base. The seeds therefore cannot fall out without some movement of the capsule. The thin wiry stem - ~~which gives the plant its common name -~~ is easily moved by wind or touch, and moves jerkily in such a way that seeds will be thrown out of the capsule. This of course is what has classically been described as the censer mechanism of seed

dispersal. However, this in itself, without subsequent wind dispersal, is unlikely to scatter the seed far from its source of origin.

The seeds are small, brown, smooth, and spindle-shaped, from 0.69mm to 1.218mm in length, and 0.383mm to 0.527mm in breadth. They weigh from 56 µg. to 131 µg. They are thus quite small and light, but have no obvious adaptions for wind dispersal (Pijl 1969).

Seed-eating and aquatic birds have been shown to carry seeds of some species over great distances (Gillham 1970). However, I have found no references to Campanula seed having been found in bird crops or droppings. Also I have seen no reports of birds having been seen feeding on Campanula capsules.

Ridley (1930 p.360) reports that viable C.rotundifolia seed has been recovered from horse dung. It would therefore seem that dispersal in the gut of large herbivores, which have eaten the ripening capsules, might be a most efficient means of long distance seed dispersal. He also quotes Praeger, who records that C.rotundifolia seed will float for one day before sinking, and suggests that "no doubt all the species of the genus are dispersed mainly by rain-wash and to some extent by wind". At Fountains Abbey seed was found to have been dispersed to more than 6m (20ft) from the parent plant (Ridley l.c.p.28). However, from my own observations on the occurrence of seedlings, there is no doubt that by far the majority of the seed is deposited in the immediate vicinity of the parent plant.

SECTION 6 - SEED GERMINATION

As revealed by the study of wild seed collection and progenies from crossing experiments, germination in C.rotundifolia is often highly erratic.

Methods of studying seed germination

About 100 seeds were sown on germinating pads in petri dishes, and kept moist for three weeks on an illuminated bench. Seeds germinating within this time were removed. The germinating pads were then allowed to dry out, and

TABLE 7.4

THE PERCENTAGE GERMINATION OBTAINED ON THREE SUCCESSIVE SOAKING-DRYING CYCLES

(All but one of the examples quoted are of seed from artificial hybridisations as, in most cases, only small numbers of each sample of wild collected seed were sown.)

Female Parent		Male Parent		2n	Percentage germination on successive soakings			Total Percentage
					1st	2nd	3rd	
41.6.C	Muir of Ord	64.6.B	Campsies	4x	85	6	0	91
45.6.A	Carrbridge	64.6.B	Campsies	4x	15	60	0	75
38.6.I	Blair Atholl	45.6.A	Carrbridge	4x	13	23	44	80
89.6.C	Arrochar	64.6.B	Campsies	4x	53	24	12	89
89.6.C	Arrochar	38.6.F	Blair Atholl	4x	51	35	13	89
45.6.B	Carrbridge	61.6.E	Strontian	6x	91	5	0	90
1.6.A	Oban	2.6.A	Oban	6x	43	9	0	51
74.7	Isle of Man	Wild collected seed		6x	100	0	0	100

left dry for a week before re-wetting for a further three weeks. Germinating seeds were removed as before. The process was repeated a third time, and the percentage of seed germinating on each soaking calculated (table 7.4).

On the first soaking, there was a flush of germinating seeds after 5-7 days. This rapidly tailed off, so that in the third week hardly any seeds germinated. However, a careful examination of the remaining ungerminated seeds suggested that many were still viable. Keeping the seeds continually moist, either at laboratory temperatures or with a period of up to 14 days at 2°C in a refrigerator, resulted in little further germination. Drying and resoaking however usually resulted in a further flush of germination, with a rapid tailing off as before. Even after three such soakings some apparently viable seed often remained ungerminated. Further soaking-drying cycles rarely brought about any further germinations, but removal of that part of the testa which overlies the micropyle often caused a few of the remaining seeds to germinate.

This technique was found by Amen (1967) to be the only reliable method of obtaining a high germination percentage with obviously good seed of Luzula spicata. I have repeated some of his experiments with L.spicata and have obtained similar results. I have also found that it is the only method of obtaining any germination at all in Bartsia alpina, in which germination percentages up to 90% have been obtained. Similar spectacular results have been obtained with Elymus arenarius and Archangelica officinalis. Interestingly, however, seed of C.rotundifolia does not behave in the same way, only 5 to 10 percent of the remaining apparently viable seed germinating after treatment.

It can be seen from table 6 that the wild collected seed of an Isle of Man hexaploid all germinated at the first soaking. This however was exceptional, most seed, whether collected in the wild or derived from a controlled cross,

requiring several soaking and drying cycles to reach a high percentage germination. In some cases, however, many apparently viable seed may remain ungerminated through several cycles in which no germination occurred. Dry storage for several months followed by a further soaking may cause a few more seeds to germinate, but many seem to be very deeply dormant. It proved impractical to continue most germination tests beyond the third soaking, even if some of the seed was suspected of being potentially germinable, as fungal infection became a major factor in some plates.

SECTION 7 - DEVELOPMENT FROM SEEDLING TO ADULT PLANT

The first stage in germination is usually the emergence of the radicle, which reaches several millemetres in length before the cotyledons appear from within the testa. The testa is very soon shed. A frequent anomaly (2-3%) in most batches of germinating seed is the occurrence of seedlings in which radicle growth is weak or totally suppressed. In the most extreme cases no radicle ever emerges from the testa, only a hypocotyl bearing two cotyledons growing from the seed coat, which remains attached to the base of the hypocotyl. Where this anomaly occurs with a high frequency (tables 10.9, 9.5, 9.7) it can be assumed that there is some degree of cross - or self-incompatibility between the parents.

Other seedling anomalies suggesting such incompatibility are the occurrence of chlorotic and variegated seedlings (table 9.3).

On germination, a seed of C.rotundifolia gives rise to a typical dicotyledon seedling with two heart-shaped to oblong cotyledons (fig.7.13). The first post-cotyledonary leaves are of the basal, cordate type, and are produced in a rosette. Under favourable conditions the buds in the axils of the first 1-3 rosette leaves produce secondary rosettes (fig.7.1) while those in the axils of later rosette leaves usually produce flowering stems (fig.7.2). The

rosettes bear only cordate leaves, while the flowering stems nearly always bear only linear leaves, with spathulate intermediate leaves towards the base of the stems.

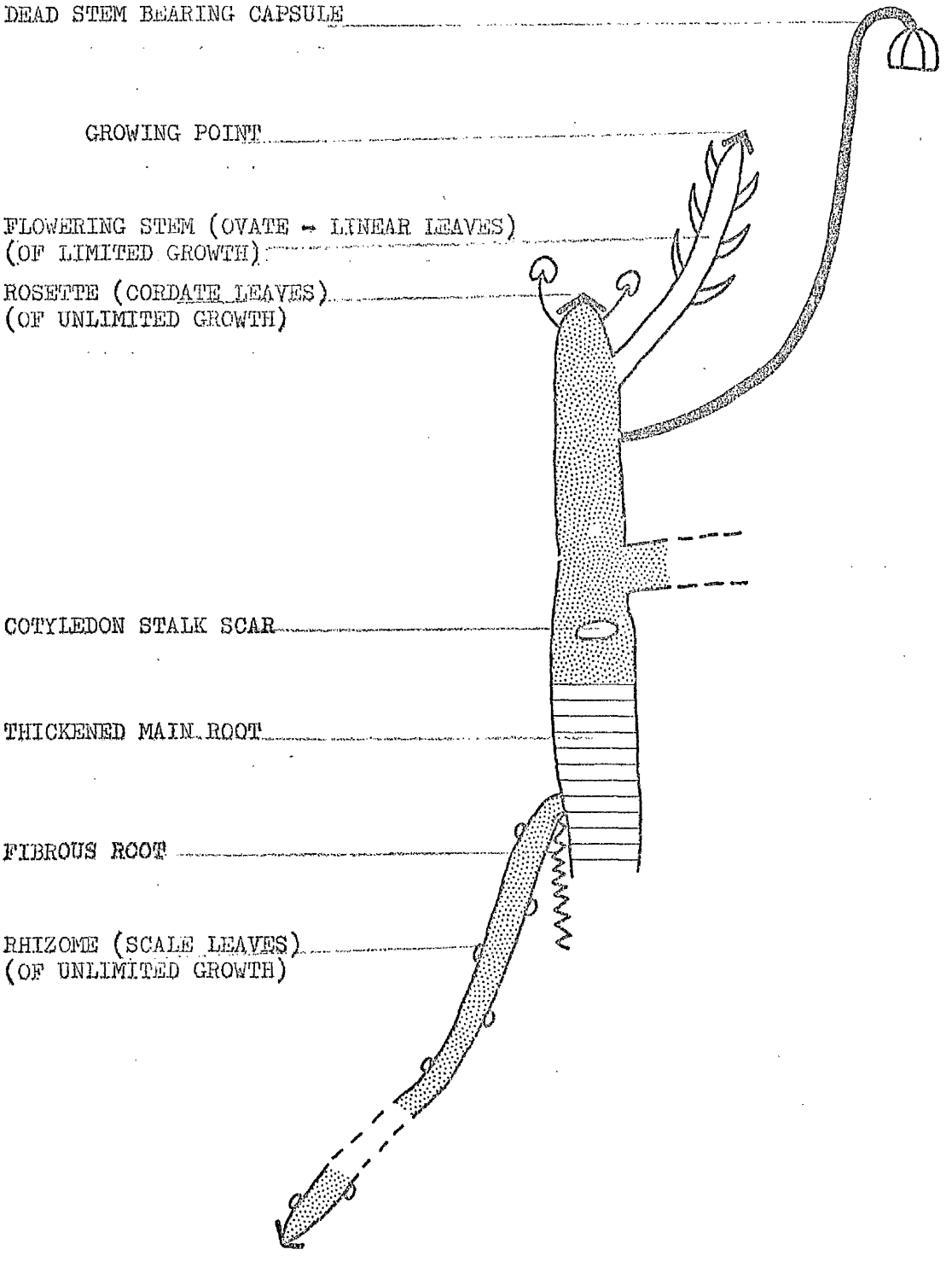
The main axes of the rosettes elongate very little, but bear in the axils of their cordate leaves, elongated flowering shoots (fig.7.3) and sometimes shoots which develop into rhizomes (figs 7.4 and 7.5). These rhizomes have very long internodes and bear only scale leaves, or rarely (probably if they receive some light,) cordate leaves (fig.7.4).

The tap root quickly develops into a carrot-like white main root. In many cases it is this alone which gives rise to the rhizomes (fig 7.6), none arising from the aerial shoots. Though the tap root is usually very long lived, the primary rosettes rarely live for more than 2 years, the growth of the plant being continued by the rhizomes (fig.7.4). Secondary major roots sometimes arise from the original shoot (fig.7.6) or a rhizome branch (fig.7.9).

The rhizomes may be branched or unbranched. The thicker, stronger branches usually give rise directly to flowering stems, unlike the thinner, weaker branches which give rise to rosettes (fig.7.7). Such rosettes behave in exactly the same way as the primary rosette, producing axillary flowing shoots (fig.7.8). Further rhizome branches are usually produced from the axils of rhizome scale leaves (fig.7.8), not as adventitious shoots from a main root. Roots are rarely borne on young parts of a rhizome system, unless they become disconnected, only occurring on the older mature parts (figs 7.8 and 7.9).

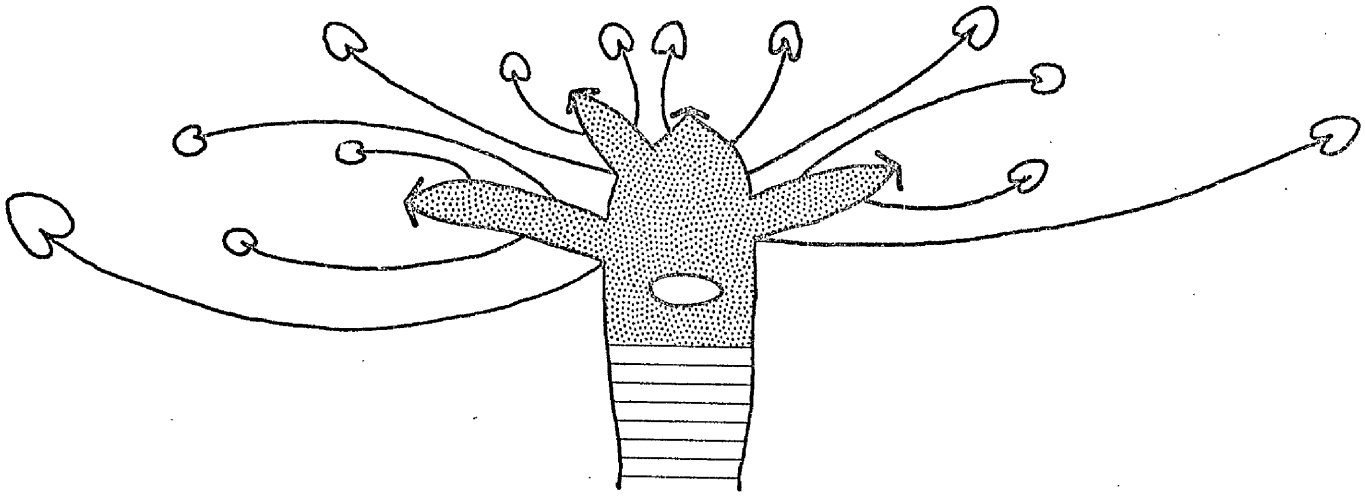
In summary, the seedling gives rise to a primary rosette which produces flowering shoots and rhizomes (either from the rosette or adventitiously from the tap root). The rhizomes then grow to produce a rhizome system, whose branches either grow directly into flowering shoots, or form secondary rosettes which repeat the behaviour of the primary rosette.

KEY TO FIGS. 1 - 9



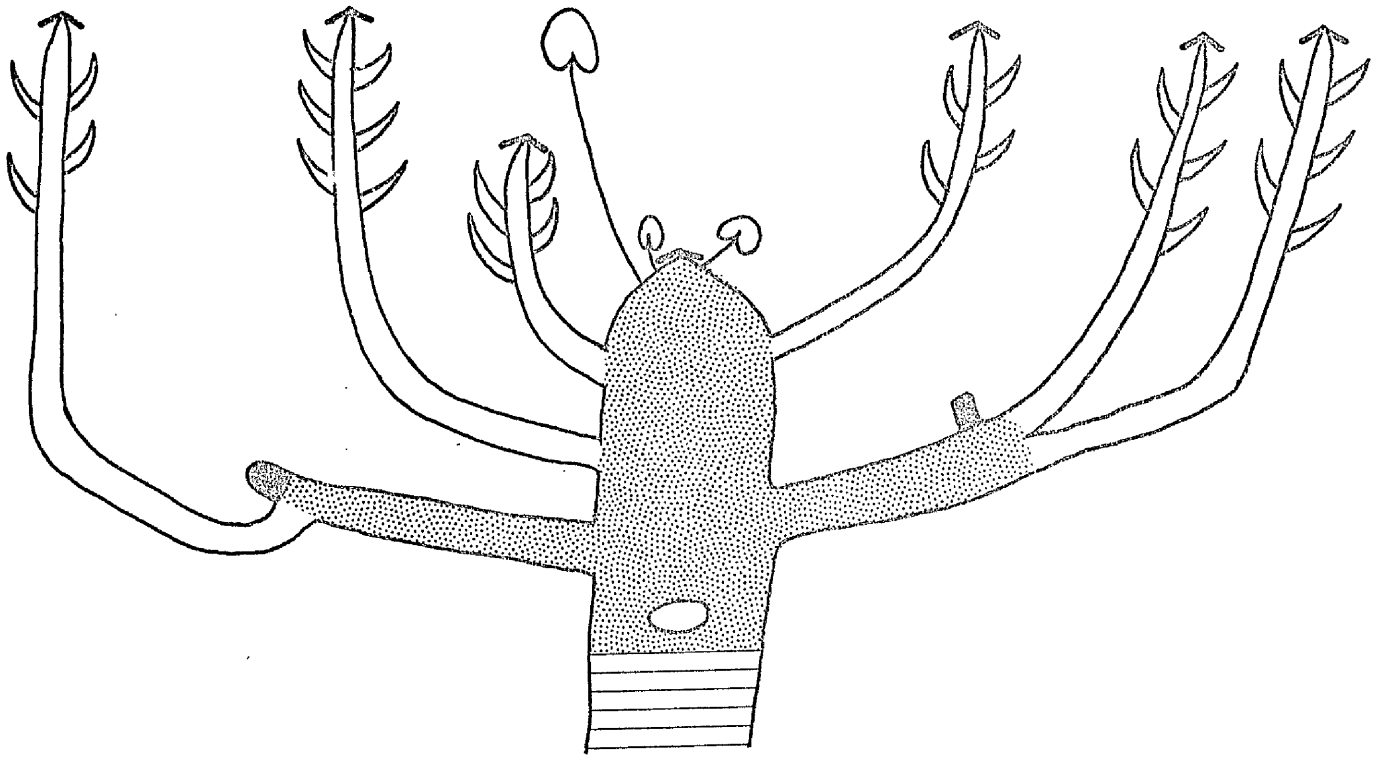
UNSHADED:	STEM OF LIMITED GROWTH
LIGHTLY SHADED:	STEM OF UNLIMITED GROWTH
HEAVILY SHADED:	DEAD
STRIPPED:	THICKENED ROOT
ZIG-ZAG:	FIBROUS ROOT

FIG. 7.1



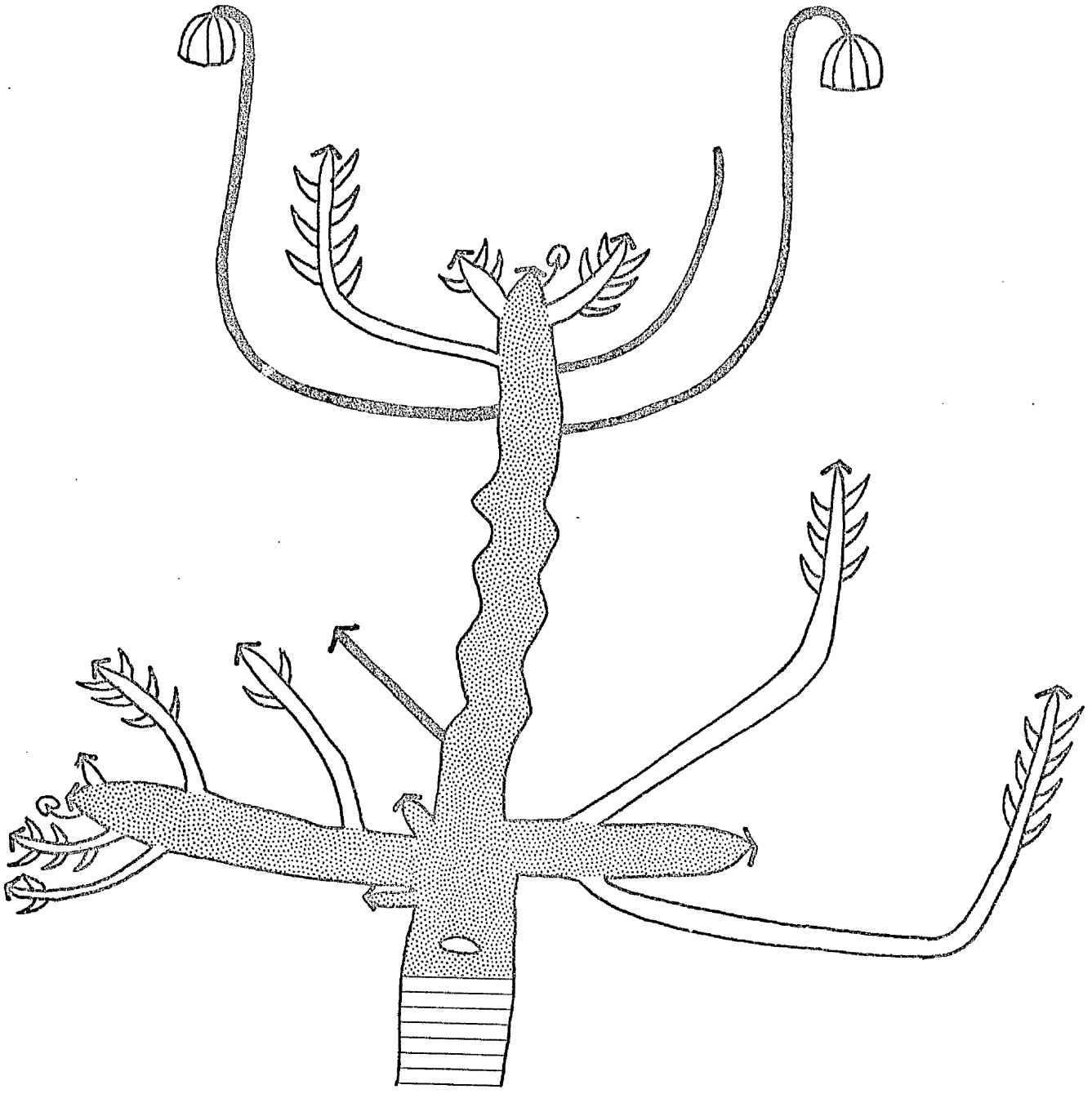
2 MONTH OLD SEEDLING WITH PRIMARY ROSETTE AND 3 AXILLARY ROSETTES

FIG. 7.2



1 YEAR OLD PLANT ENTERING ITS SECOND GROWTH SEASON. AXILLARY ROSETTE APICES HAVE DIED.

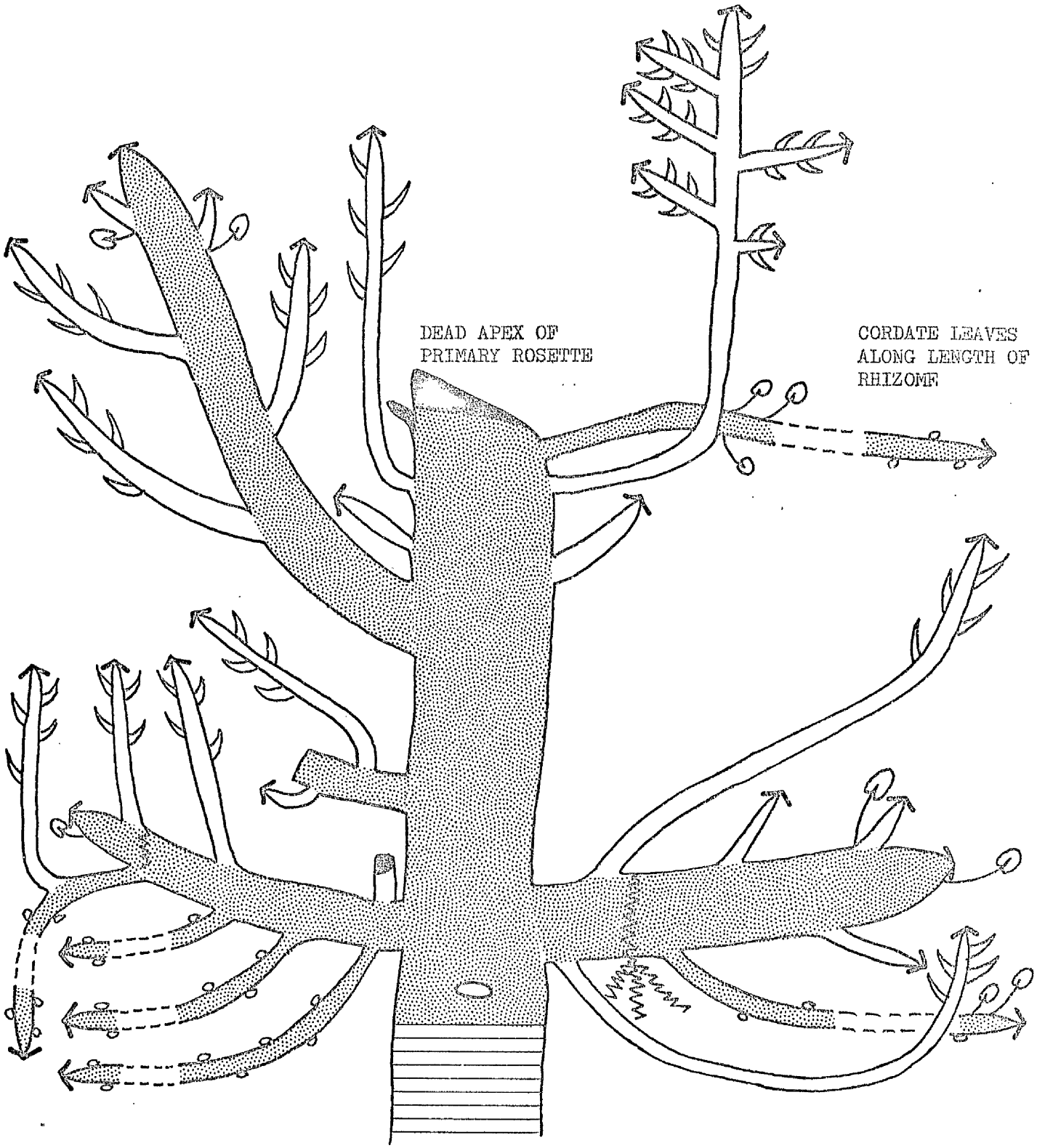
FIG. 7.3



1 YEAR OLD PLANT ENTERING ITS SECOND GROWTH SEASON.

IT HAS PRIMARY ROSETTE BEARING THE REMAINS OF PREVIOUS YEAR'S FLOWERING STEMS, AND PRIMARY AND AXILLARY ROSETTES BEARING YOUNG FLOWERING STEMS. NOTE 2 YOUNG SECONDARY ROSETTES ARISING AT BASE OF OLDER AXILLARY ROSETTE.

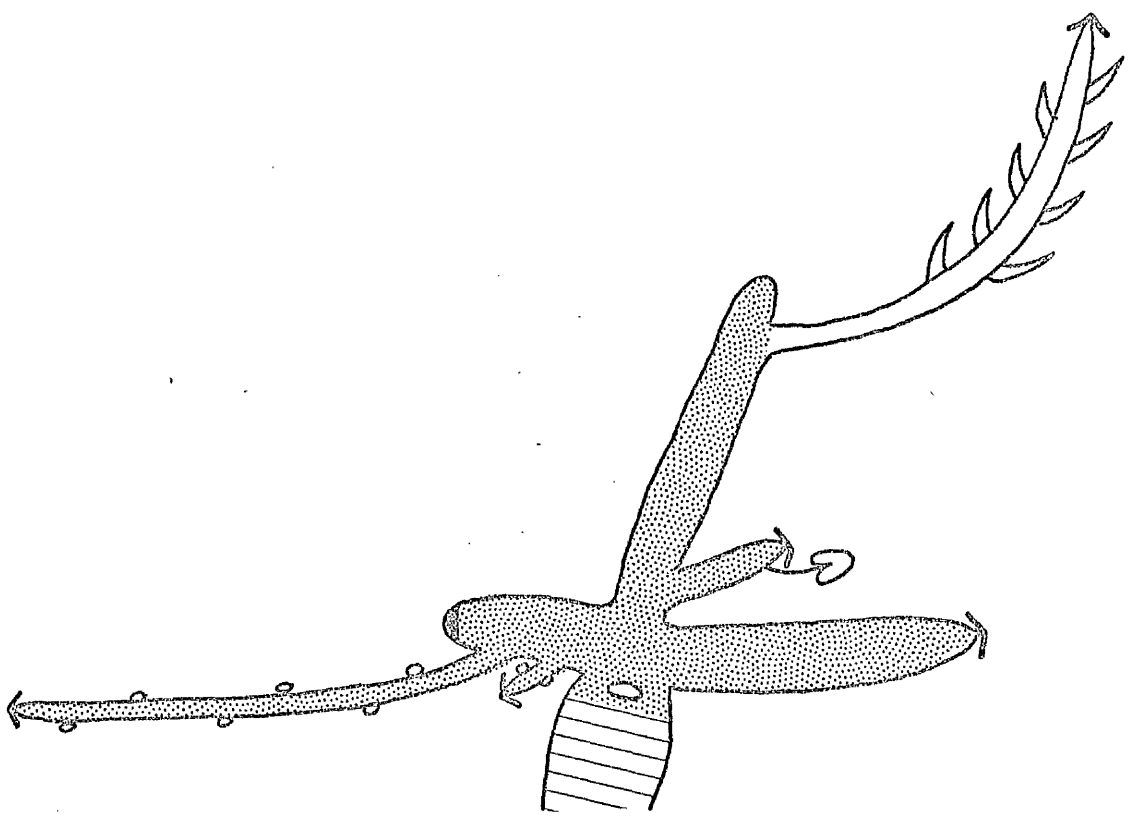
FIG. 7.4



1 YEAR OLD PLANT ENTERING ITS SECOND YEAR OF GROWTH.

VERY VIGOROUS PLANT. ALL RHIZOMES ARISING FROM AERIAL SHOOTS.

FIG. 7.5



1 YEAR OLD PLANT ENTERING ITS SECOND GROWTH SEASON.

A DEPAUPERATE PLANT WITH 2 OF ITS 4 ROSETTE APICES DEAD. RHIZOMES ARISING FROM AN AERIAL ROSETTE.

FIG. 7.6

1 YEAR OLD PLANT ENTERING ITS SECOND GROWTH SEASON.

VERY VIGOROUS PLANT. ROOTS ARISING FROM AERIAL PARTS OF STEM. ALL RHIZOMES AND SOME FLOWERING STEMS ARISING ADVENTITIOUSLY FROM TAP ROOT AND THICK ADVENTITIOUS ROOT.

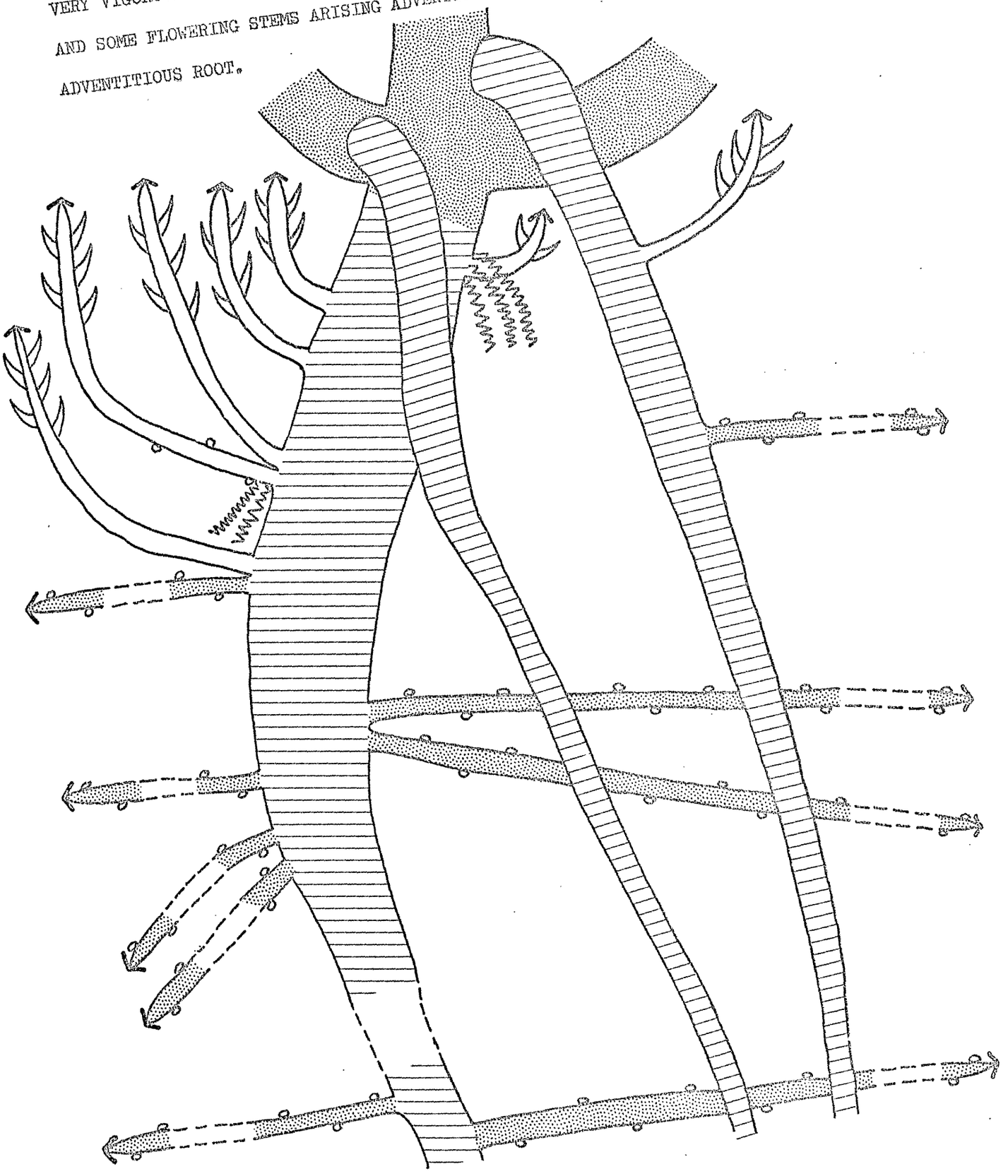
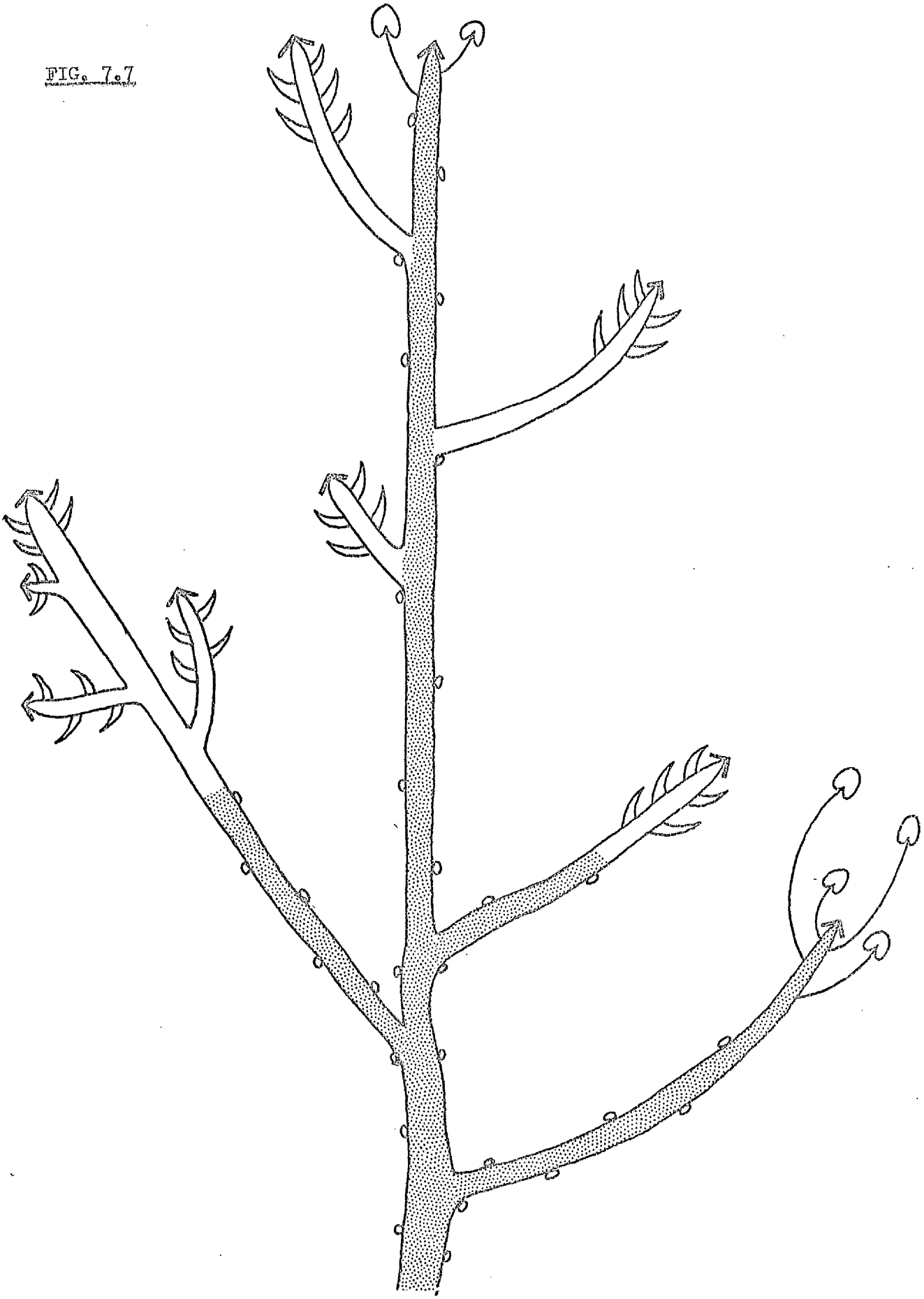


FIG. 7.7



PART OF AN EXTENSIVE RHIZOME SYSTEM WITH STRONG BRANCHES GIVING RISE DIRECTLY TO FLOWERING SHOOTS WHILE WEAKER BRANCHES GIVE RISE TO ROSETTES.

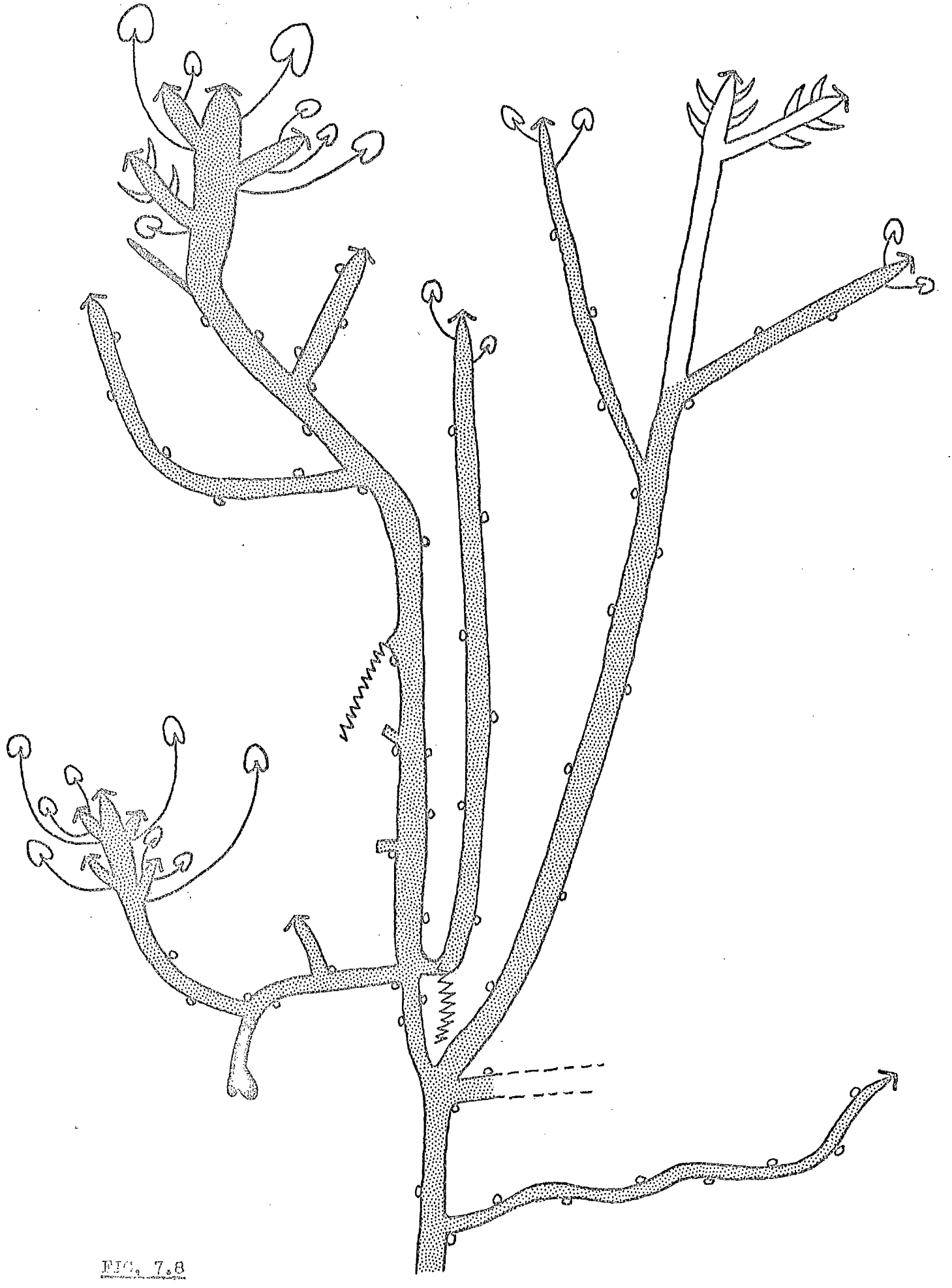
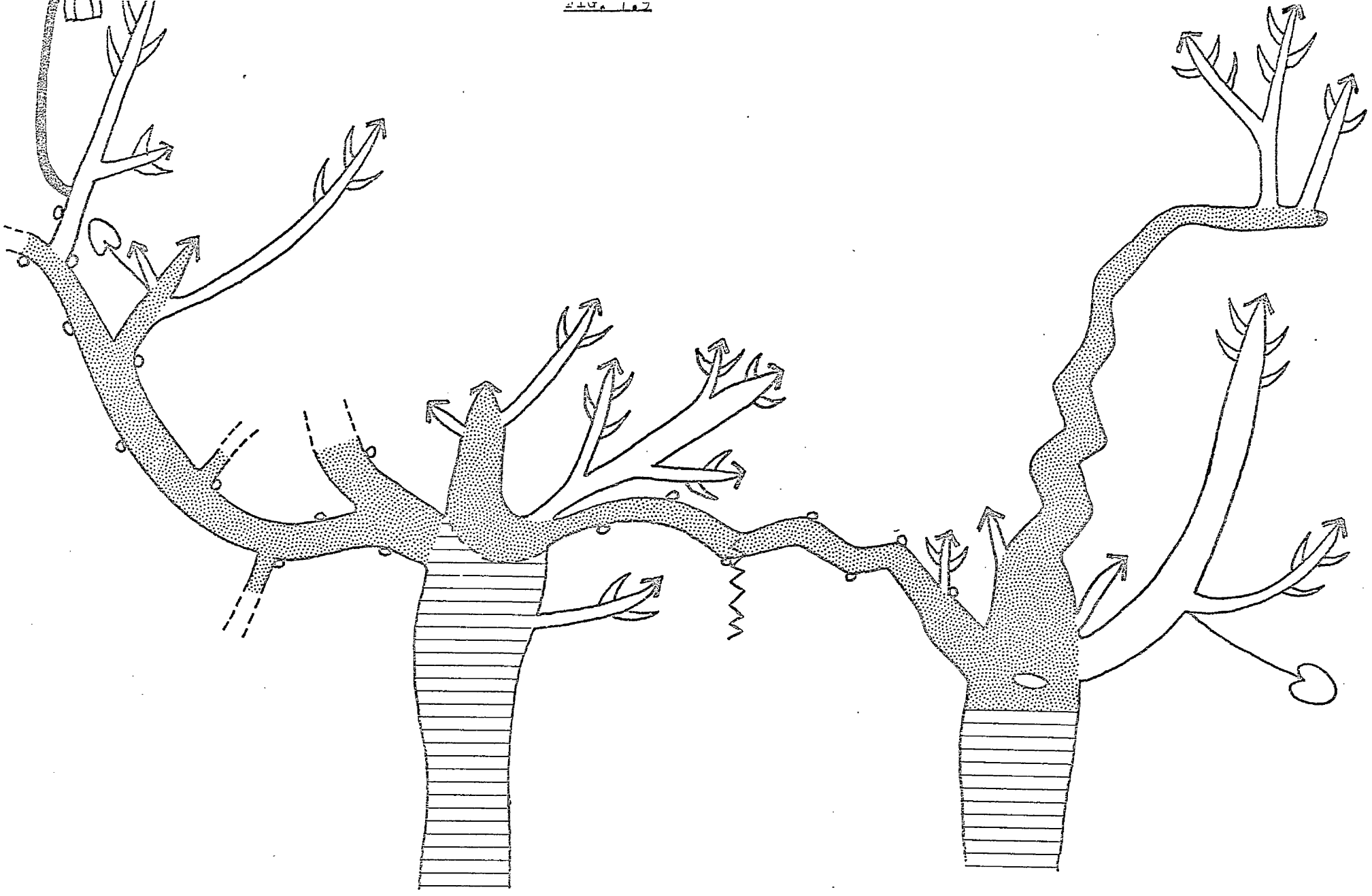


FIG. 7.8

PART OF EXTENSIVE RHIZOME SYSTEM WITH ROSETTES GIVING RISE TO SECONDARY ROSETTES AND A FLOWERING STEM.



3 YEAR OLD PLANT ENTERING ITS 4th GROWTH SEASON. ROSETTE FORMED AT APEX OF RHIZOME BRANCH HAS DEVELOPED A MAJOR THICKENED ROOT.

The diagramatic illustrations of the shoot system (figs 7.1 - 7.9) represent the spring condition. In winter the aerial shoots die back, leaving the rhizome system with growing points terminating either in rosettes, or in tufts of linear-spatulate leaves which will develop directly to flowering shoots. Green leaves are always present above the surface of the soil, and no distinct overwintering buds are produced.

In the light of the above observations I cannot agree with Podlech (1965) when he states that the Heterophylla are characterised by overwintering buds which never develop directly into flowering shoots. This may be true of some of the non-rhizomatous southern European plants, which I have never grown, but it does not apply to C.rotundifolia, C.gieseckiana, C.cochleariifolia, C.scheuchzeri or C.ficarioides. The rosettes of the Heterophylla, however, never grow out directly to flowering shoots as in C.percisifolia. The flowering shoots always arise from an axillary position in a rosette or terminally on a rhizome branch.

As reported in Chapter 5 there is considerable variation in the extent of rhizome development in different clones. As this is often habitat correlated it has probably come about through natural selection.

The one diploid Greenland plant of C.gieseckiana has relatively short stout rhizomes, and this character is shared by most of the hexaploid plants I have grown. In particular, plants from the sea cliffs near Oban (topodemes 1.6, 2.6 and 55.6) tend to have very short stout rhizomes, as do plants from the Merrick (13.8), and it is interesting to note that these are the populations which bear the greatest morphological resemblance to C.gieseckiana. The plant with the least rhizome development, and in which all shoots appeared to be strongly negatively geotropic, was a member of a hexaploid population, which was otherwise quite strongly rhizomatous, growing on the schist cliffs of Muckanaght in Connemara in western Ireland (fig.5.2). The single Canadian hexaploid (97.6 fig.7.11) was similar to this Irish plant in its rhizome

FIG. 7.11 Hexaploid from the Isle Gaspé in the St. Lawrence estuary in east Canada (97.6).

growth (though with much more erect shoots), as were some Austrian plants of C.scheuchzeri. All these plants were rather difficult to retain in cultivation without special attention; winter dampness and fungal attack or insect attack destroyed the dense rhizome system which lacked the far creeping branches that enabled other clones to survive such conditions. Tetraploid plants tended to have more extensive rhizome systems than the hexaploids.

Despite the above mentioned differences between tetraploids and hexaploids, ecologically correlated differences in rhizome development were noticed which were common to both cytodemes. Sea cliff plants as a whole had relatively short rhizome systems, while grassland, and especially sand dune plants, tended to have very strongly developed rhizome systems.

SECTION 8 - THE OCCURRENCE OF SEEDLINGS IN THE FIELD

All sites from which mature plants were taken were examined to see if seedlings were present, although in some cases only the turf collected was carefully scrutinised.

Seedlings of C.rotundifolia with post-cotyledonary leaves are fairly easily distinguished, but when only the cotyledons are present it was usually felt necessary to confirm the identification by breaking a cotyledon and looking for the characteristic milky exudate from the veins.

The primary seedling root always forms a thick, cylindrical tap root, from the upper regions of which rhizomatous shoots emerge. These rhizomes may be long or short, depending on the ecodeme, the very short type being rare. The long rhizomes rarely develop roots similar to the original tap root. On the short rhizomes, which occasionally produce such roots, the roots are always in clusters beside the original tap root. It is therefore nearly always possible to tell if a given plant has originated as a seedling at a particular site or arrived there by rhizomatous spread. For relatively small plants which possess a tap root it is often possible to arrive at an

approximate age by examining the degree of rhizome development, though of course rhizome formation may be greatly delayed in the case of small, weak plants growing in the shade.

Seedlings were found at only *eight* sites, and, though they may have been overlooked elsewhere, they are probably not very common as seedling establishment seems to require rather special conditions. These would seem to be primarily the absence of competition in a microhabitat with more or less permanently moist surface soil. These conditions are necessary as the small seedlings grow relatively slowly. Many seeds probably germinate in spring, (March-April) and are therefore beginning their development at what is often a dry time of year, and when the surrounding plants are beginning to grow rapidly.

Details of the localities in which seedlings have been found are given below, along with notes on the condition of the plants.

1) Seaside cliff ledges, Ardlamont Point, near Tighnabruich, Argyll, 16/988642. Site examined 29/3/1967 (3/7), 12/4/1968 (3/8), 22/7/1969 and 10/4/1971. C.rotundifolia is a common plant on the cliffs in this locality, growing in cracks and on ledges, and to a limited extent in the grassland above the cliffs. The vegetation is very diverse, ranging from highly calcareous wet flushes with tall herb vegetation, through species rich grassland, to dry acid ledge vegetation with Erica cinerea dominant. The Campanula is more or less confined to the calcareous habitats. There is little evidence of grazing by large domestic herbivores, probably because of the inaccessibility.

In March 1967 many seedlings at the cotyledon stage, were seen on areas of bare soil, while in April of the following year some seedlings were noticed in a wet tussock of the moss Cratoneuron filicinum (figs 7.12 and 7.13). In

FIG. 7.12 Seedlings growing on wet Cratoneuron filicinum at Ardlamont, Tighnabruaich, Argyll (10.4.1971)

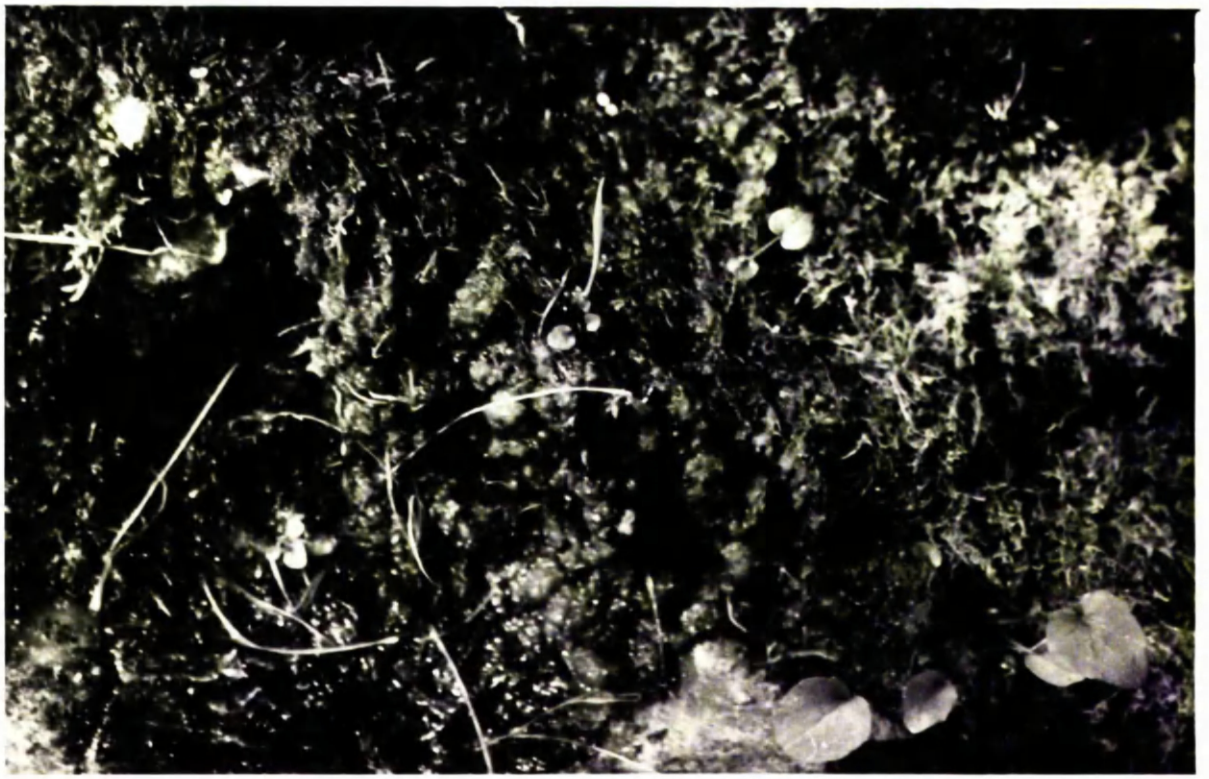


FIG. 7.13 Seedlings growing on green algal jelly at Ardlamont. At upper left are two very young seedlings, one with cotyledons only, the other with one post-cotyledonary leaf. Another seedling with cotyledons only is visible at top centre. Four older seedlings are present.

this flush the moss had a cover value of almost 100%, but other species growing in the tussock besides the Campanula seedlings were :-

Cratoneuron filicinum (dominant)
Centaurea nigra (mature plant)
Filipendula ulmaria
Samolus valerandi (small rosettes and seedlings)
Umbilicus rupestris
Conocephalum concium
"Palmella" green algal slime

In July 1969 I decided to carry out a more thorough survey of the micro-habitats in which seedlings occurred, and to look to see if any 1-3 year old plants were present. The habitats in which seedlings and young plants were found are given below :-

Habitats in grassland on steep slope above cliff

(a) One small etiolated seedling (cotyledon and one post cotyledon leaf) in fairly dense grass sward with :-

Anthoxanthum odoratum
Campanula rotundifolia (mature plant)
Erica cinerea
Galium saxatile
Hieracium sp.
Hypochaeris radicata (seedling)
Potentilla erecta
Mnium hornum
Cladonia spp. (squamules)

(b) C.rotundifolia seedlings on bare patch of soil about 10cm in diameter in vegetation described in 1. with :-

Hypochaeris radicata
Thymus drucei (seedling)
Bryum sp.
Eurhynchium praelongum
Cladonia spp. (squamules)

Habitats on cliff ledges

(c) One seedling on moss tussock with :-

Amphidium mongeottii
Campylium stellatum
Riccardia pinguis

(d) One seedling on moss tussock with :-

Cratoneuron filicinum
Cerastium ~~holosteoides~~ fontanum

(e) One seedling on moist soil with :-

Arrhenatherum elatius (seedling)
Cratoneuron filicinum

(f) One seedling among old, dead Arrhenatherum stem bases, the lower parts covered with "Palmella" green algal slime with :-

Arrhenatherum elatius (one live shoot)
Campanula rotundifolia (living, but leafless, old rhizome)
Cratoneuron filicinum

(g) One seedling in another habitat similar to (f).

(h) Two one-year old seedlings (which must have germinated in autumn), each with about four well-developed leaves borne on a single rosette on a rock ledge with :-

Anthoxanthum odoratum (one seedling)
Cratoneuron filicinum
Eurhynchium praelongum
Conocephalum conicum
Pellia ephiphylla

(i) One two-year old plant (single rhizomatous branch bearing about three leaves) on a wet ledge with :-

Amphidium mongeottii
Cratoneuron commutatum
Pellia neesiana
Riccardia pinguis

When these data were examined it was realised that they did not give enough information to determine the time of germination. The site was therefore re-visited in April 1971, with special attention being paid to the size of the seedlings and the number of postcotyledonary leaves.

(j) Five seedlings with cotyledons or cotyledon stalks and 0,2,3,5 and 6 post-cotyledonary leaves respectively. A second year plant was also present. On mud with :-

Festuca rubra
Bryum cf. pseudotriquetrum
Fissidens taxifolius
Pellia neesiana

(k) One seedling with cotyledons only. One second year seedling and one young plant in at least its third year. On soil with :-

Arrhenatherum elatius (1 seedling)
Plantago maritima (2 seedlings)
Pellia neesiana
Riccardia multifida
"Palmella"

TABLE 7.5

SUMMARY OF THE DEVELOPMENTAL STATE OF SEEDLINGS IN COLLECTIONS j-n FROM ARDLAMONT POINT, TIGHNABRUAICH, ARGYLL ON 10TH APRIL 1971

No. of post-cotyledonary leaves	0	1	2	3	4	5	6	7
No. of individuals	3	1	2	2	0	1	1	1

(l) Two seedlings with the remains of cotyledonary petioles and two and three post-cotyledonary leaves respectively. On Crateneuron commutatum turf with :-

Arrhenatherum elatius (1 young plant)
Brachypodium sylvaticum
Endymion non-scripta (2 second year seedlings)
Filipendula ulmaria (1 young plant)
Schoenus nigricans (3 young plants)
Campylium chrysophyllum
Pinguicula vulgaris
Riccardia multifida
"Palmella"

(m) One seedling with cotyledons and one post-cotyledonary leaf.

(n) Two seedlings, one with cotyledons only, the other with cotyledonary stalks and two post-cotyledonary leaves.

See summary of data in table 7.5.

2) Rough mountain pasture, Creag Tharsuinn, Argyll. 425m (1,750ft) 26/084907 2/8/1969 C.rotundifolia occurs occasionally in the grassland and on rock ledges and cracks in cliffs. Grazing pressure is probably fairly heavy. One young plant was estimated to be in its second year. It had no rhizome development. It had a well developed rosette of leaves about 3 inches in diameter. On small soil cliff about 6 cm high with:-

Dicranella heteromalla
Nardia scalaris

Surrounding vegetation (species bordering soil patch)

Agrostis canina
Festuca vivipara
Galium saxatile
Nardus stricta
Potentilla erecta
Seglingia decumbens
Trichophorum caespitosum
Vaccinium myrtillus
Sphagnum papillosum

3) Clay on limestone ledge in gorge. Cassop, County Durham. Three second year seedlings with Sesleria caerulea

4) Mountain streamside in rough grassland. Ben Alder, Inverness-shire. 675m (2,250ft), 4/8/1970. C.rotundifolia occurs occasionally on streamsides and rock ledges. Grazing is probably negligible. The only large herbivores seen in the area were Red Deer, and in the summer they kept to the higher ground.

(a) Two seedlings with cotyledons and one post-cotyledonary leaf on small vertical soil cliff on the bank of a stream (fig.7.14) among stems of Nardia scalaris. Other species on the soil cliff (within 30cm of seedlings) :-

Potentilla erecta (seedling with one post-cotyledonary leaf and etiolated-hypocotyl 3.5cm long)
Hypnum cupressiforme
Sphagnum subsecundum
Caly poegia muelleriana
Diplophyllum albicans
Pellia neesiana

Surrounding vegetation overhanging soil cliff :-

Agrostis canina
Alchemilla alpina
Calluna vulgaris
Campanula rotundifolia (flowering)
Carex binervis
Deschampsia caespitosa
Festuca vivipara
Nardus stricta
Potentilla erecta
Vaccinium vitis-idaea

(b) One seedling with one post-cotyledonary leaf, on flat mossy streamside bank with :-

Alchemilla alpina (seedling)
Campanula rotundifolia (two rosettes)
Hylocomium splendens
Hypnum cupressiforme
Plagiothecium undulatum
Rhytiadelphuus loreus

One seedling with two post-cotyledonary leaves as above with :-

Oligotrichum hercynicum
Diplophyllum albicans

On same soil patch :-

Blechnum spicant
Campanula rotundifolia
Poltrichum sp.(commune or alpinum
Plagiothecium undulatum

Surrounding vegetation :-

Agrostis canina
Calluna vulgaris
Carex binervis
Deschampsia caespitosa
Euphrasia sp.
Potentilla erecta
Trichophorum caespitosum
Vaccinium myrtillus
Viola viviniana
Diplophyllum albicans

5) Roadside ditch in scrubby woodland, 6m (20ft), Carry, near Tighnabruaich, Argyll, 16/9 22/3/1969.

A few plants of C.rotundifolia occur on a raised beach on the seaward

FIG. 7.14 Single seedling with cotyledons and one post-cotyledonary leaf on steep streamside bank at 675m (2250ft) on Ben Alder, Inverness.

side of the road, and on the verge and ditchside on the inland wooded side. Seedlings were only found on the bank between the ditch and the wood - the only site in which there was an area of unvegetated moist soil.

Three seedlings, each with one post-cotyledonary leaf, were found on a small (4cm high) vertical soil cliff with :-

Mnium longirostrum
Thuidium tamariscinum

One seeding with one post-cotyledonary leaf was seen on bare soil about 5mm deep overlying bed rock. The bare patch was at the entrance to a disused vole's burrow. Associated species on the bare soil patch were :-

Anthoxanthum odoratum (seedling)
Betula pubescens (seedling)
Centaurea nigra (seedling)
Mnium hornum
Thuidium tamariscinum

The ditchside vegetation surrounding the bare soil patches consisted of :-

Herb layer

Agrostis canina
Centaurea nigra
Hedera helix
Lonicera periclymennum
Campanula rotundifolia
Oxalis acetosella
Potentilla erecta
Primula vulgaris

Tall herb layer

Corylus avellana (young shrub)
Pteridium aquilinum

Tree layer

Quercus robur

6) Clayey, gravelly fluorspar detritus, 390m (1,300ft) Sedling mine, Cowshill, Weardale, Co. Durham. Grid ref. 35/359412. Pop.14/70. 16/9/1970.

Mine spoil heaps around old workings, with the degree of vegetation varying from totally absent to more or less complete cover, but with much bare soil under the vegetation.

(a) Base of steep, very unstable, unvegetated slope, where some stability is given by the presence of a culvert emerging from under the pile of detritus.

Many seedlings with cotyledons and one or two post-cotyledonary leaves.

Second year and older plants were also present.

Associated species :-

Festuca rubra	Minuartia verna
Hieracium vulgare agg.	Rumex acetosa

(b) More stable slope with many seedlings and young plants of all ages.

Associated species :-

Agrostis tenuis	Bryum sp.
Festuca ovina (dominant)	Hypnum cupressiforme
Festuca rubra	Weissia sp.
Thymus drucei	Cladonia squamules
Viola lutea	Cornicularia aculeata

(c) As above (fig.7.15)

Associated species:-

Agrostis tenuis	Hypochaeris radicata
Anthoxanthum odoratum	Minuartia verna
Equisetum arvense	Thymus drucei
Hieracium vulgare agg.	

7) Compacted sand in dune system where sand extraction had taken place. 6m (20ft), near Crago, Luskentyre, S.Harris, Outer Hebrides (Inverness). Pop.58/7. 24/8/1967. Grid. ref. 08/9---9---

Several dozen very vigorous second year plants were coming into flower. C.rotundifolia was dominant, with the associated species being :-

Bellis perennis	Poa pratensis
Carex flacca	Thymus drucei
Festuca rubra	

8) Agrosto-Festucetum. South of Nameless Sike, near Cow Green, Upper Teesdale, Co. Durham, c.l.630ft. Grid ref. 35/907295. 6/1969. 12/5/1969.

Second year plant present.

Discussion of sites in which seedlings occur

Sites (1) - (3) can be regarded as wholly natural, while sites (4) - (8) have been disturbed in varying degrees by human activities. From the descriptions of the 8 sites in which C.rotundifolia seedlings were found, it can be seen that they were found only in very open microhabitats. Only in site 1a was a seedling found in a habitat in which vascular plants had a cover value of 100%, and that seedling was very etiolated and of an unhealthy

FIG. 7.15 Numerous young plants on spoil heap at fluorspar mine, Cowshill, Weardale.

yellowish green colour. All the other seedlings found were on bare moist soil or moss tussocks, often in very shady places. Though often etiolated (the hypocotyl in the seedling in site 3a fig.7.14, was 1cm long), the seedling leaves are usually a deep green colour. In such places growth may initially be very slow (e.g. 1i), but by rhizome development, the plant can spread to better illuminated neighbouring areas more suited to the vegetative growth and flowering of the mature plant. Rhizomes up to about 50cm long with only scale leaves along their lengths and a rosette of foliage leaves at one end (i.e. which have been produced within one growing season), have been seen in the wild in cracks on mountain cliffs. In this way C.rotundifolia can reach dry rock crevice habitats ideally suited to the growth of the mature plant, but in which seedling establishment is quite impossible. C.rotundifolia, with its deep roots and rhizomes, is one of relatively few vascular plants which can colonise many very narrow dry cracks on cliff faces.

The difficulties of seedling establishment could be one of the reasons why C.rotundifolia (the hexaploid cytodeme) is absent in most of the grassland on the steep slope leading up to the most westerly cliffs of Ben Bulbin, Sligo, yet is a very common plant on the cliffs themselves and in the grassland within about three meters of the cliff. The cliff ledges are a very unstable habitat with the thin clay soil on the limestone ledges being subject to continuous erosion, and thus providing many bare soil patches. Such open areas are not found in the grassland, but the disturbance of the uppermost grassland by deposition of material eroded from the cliffs above may be of importance in allowing the colonisation of this small area. The mature plants as well as the seedlings of the hexaploid cytodeme may require open habitats for their survival. One would otherwise have expected C.rotundifolia to have spread further downhill by vegetative spread alone.

In more open habitats (e.g. 2,6 and 7) growth may be much more rapid, though flowers are probably rarely produced till the second year. In cultivation flowering plants can be obtained within four months of sowing.

SECTION 9 - SEED GERMINATION IN THE WILD

From table 7.5 it can be seen that in April 1971 all stages were present between newly germinated seedlings with only cotyledons, and seedlings in which the cotyledons had decayed and which bore up to 7 post-cotyledonary leaves. These latter seedlings had quite clearly germinated the previous autumn. However, the winter 1970-71 was particularly mild, and the site studied was situated on a mild part of the Scottish west coast, and so the proportion of seedlings surviving the winter might well be greater than usual. The lack of any obvious division into two size classes further suggests that germination occurs over a long period, rather than in an Autumn and Spring flush. Evidence of Autumn germination was also obtained from quite a different type of site on a fluorspar tip in upper Weardale (site 5). Here much of the seed seemed to have germinated immediately it was released, seedlings with cotyledons and no, one, or two post-cotyledonary leaves being frequent on the 16th of September 1970. It is clear that many seeds also germinate in spring from the occurrence of many seedlings possessing only cotyledons in the springs (March-April) of 1967, 1968 and 1971 at site 1, and the presence of plants with only one post-cotyledonary leaf in July and August at sites 5 and 4 respectively.

These results suggest that seed germination in the wild is very irregular, occurring over a long period. This is supported by evidence from germination experiments carried out in the laboratory (table 7.4).

From the results it can be seen, especially in tetraploids, that a high proportion of the seed may not germinate on the first soaking. If this phenomenon occurs in the wild it is likely to result in germination occurring over a long period. It may be that the spring flush of germination follows a dry period, such as often occurs in March, the seed having remained continuously moist over the winter.

All the seed in a capsule is not shed at one time, and seed has been found adhering to capsule skeletons as late as the 14th of December. Thus wetting and drying may occur while seed is still within the capsule. Seed within capsules has never been observed to germinate. The seed seems to retain its viability for a long time, dried seed showing good germination after five years storage at laboratory temperatures. Although there are too few results to draw any definite conclusions, it is interesting that the higher polyploid level shows a much lower degree of dormancy (table 7.4). The same situation has been found in diploid and tetraploid Tripleurospermum indorum, by Kay (pers.com.), the diploids showing greater seed dormancy.

Several other sites have been carefully searched for the presence of seedlings, especially an area of serpentine cliff and grassland in Glendarvel, which carries an extensive population of C.rotundifolia. A population sample of 17 plants showed great morphological diversity, suggesting the presence of a large number of clones, and therefore possibly the frequent establishment of new genotypes as a result of sexual reproduction. However a careful examination of many apparently suitable habitats in August 1970 and April 1971, as well as study of the turfs containing the plants which were taken into cultivation in July 1966, failed to reveal a single seedling or young plant.

The serpentine rock gives rise to a somewhat toxic soil, resulting in the cliffs and surrounding grassy slopes having a rather sparse vegetation cover. This results in numerous open microhabitats which would seem to be ideal for the establishment of seedlings. The cliff and scree habitats were rather dry, and so perhaps unsuitable for seedling establishment except in a particularly wet year. However, C.rotundifolia was common on the cliffs and screes, and seedlings of other species (especially Thymus drucei) were frequent. In the surrounding open grassland habitats which were much

disturbed by frost heaving and soil erosion, there were many small moist soil cliffs. From observation on sites 1, 3 and 4, these would be expected to be ideal habitats for seedling establishment, but despite a careful search, no seedlings were found.

In the stepped microtopography, produced by the series of small soil cliffs, C.rotundifolia tends to be particularly frequent and most vigorous at the edge of the vegetation above the small soil cliffs. C.rotundifolia was sometimes the only species present on such small soil cliffs, having grown or been washed down from the vegetation above, and being held in position by its rhizome which was connected to a rhizome network. Almost all the other species present were non-rhizomatous. Seedlings of other species (e.g. Thymus drucei and Linum catharticum) did occur in such habitats. The soil on such small soil cliffs was usually crumbly and bare of cryptogamic vegetation. This is in striking contrast to sites in which C.rotundifolia seedlings have been found, where the soil surface was usually firm and colonised by algae and bryophytes. Another factor may be that, although seed is produced, it is in rather small quantity as a result of grazing sheep and the small stature of the plants, which rarely bear more than one flower per stem. However when the site was visited in summer many C.rotundifolia flowers have been seen, and some of the cliffs and rocky areas are inaccessible to sheep. It would therefore seem that the exposed dry nature of the habitat, combined with low seed yield are the factors most likely to be responsible for the absence of seedlings. Probably seedling establishment may be possible only in the occasional year when there is no dry period during the whole Spring and Summer.

SECTION 10 - SEEDLING ESTABLISHMENT

From the above evidence of the existence of young plants in their second year and older, and the fact that some of the mature plants collected from other sites still possessed a primary tap root, it can be deduced that the

establishment of new plants from seed occurs regularly in the wild.

An interesting phenomenon has been observed in potted plants which have become contaminated with seed. Even if the original plant was large, healthy, and filled the pot, some of the contaminating seedlings grew vigorously, and if left, they replaced the original plant. Such young plants could be easily recognised, even after three years, by their vigorous, thick, carrot-shaped, white, tap roots. Thus it appeared that seedlings at least in their first two years, possess a special vigour which gives them a competitive advantage over mature plants of the same species, and probably over other species too.

An objection that could be raised to this interpretation is that, as plants from many different populations were being cultivated in the one greenhouse, the contaminating seedlings would most likely be highly outbred, and therefore show hybrid vigour. However a subjective assessment of the vigour of seedlings of known origin did not reveal any obvious differences between seedlings from wild collected seed, intra-topodeme crosses, and inter-topodeme crosses (same cytodeme). If anything, seedlings from inter-cytodeme crosses (i.e. pentaploids) were less vigorous than other seedlings, but one of the most vigorous of the contaminating seedlings was a pentaploid, produced by open pollination in the greenhouse.

Further experiments are planned to investigate this situation and to eliminate the possibility of the seedlings being more heterotic than the mature plant with which they are competing. Seed taken from a wild population will be scattered over established plants of the same population growing in pots and in beds in the garden.

No direct evidence of seedlings replacing mature plants has been obtained from the wild, but as individual clones often have characteristic flower shape, colour etc., and can therefore be recognised,

the presence of several genotypes in a single patch can sometimes be detected. One such patch near Moy, Inverness-shire, consisted of more or less evenly spaced stems covering about 2 sq.m., and was composed of light blue, very pale blue, and pure white flowered stems completely intermixed. Rhizome samples taken into cultivation yielded both very pale blue, and pure white flowered plants, and it is considered that the patch consisted of at least three clones growing closely intermixed.

SECTION 11 - THE GENETIC STRUCTURE OF TOPODEMES

This finding of the intergrowing of several genotypes is clearly of interest in considering the genetic structure of topodemes. There is evidence that certain genotypes have a degree of self-compatibility, others, however, are probably totally self-incompatible. Such self-incompatible genotypes, if they are to take part in sexual reproduction, must be growing with plants of a different genotype. A study of the genotypic structure of topodemes of C.rotundifolia, similar to those carried out by Smith (1965) and Harberd (1961, 1963) on Festuca rubra and Trifolium repens would be most interesting.

SECTION 12 - SUMMARY OF CONCLUSIONS

(1) Pollination - Cross pollination is usual, carried out mainly by bees, but self pollination may occur as the stigma lobes recurve.

(2) Breeding system - Most tetraploids are self-incompatible, but the occasional tetraploid and many hexaploids are somewhat self-compatible.

(3) Seed production - C.rotundifolia regularly produces large quantities of seed in the wild, seed or seedlings having been found up to an altitude of 675m (2,250ft). At high altitudes seed may be produced only in the occasional very favourable year, and it is at least possible that in some situations individual plants may have survived by vegetative spread for a very long time.

(4) Seed dispersal - Seed is dispersed initially by the censer mechanism, then perhaps by wind and water. Birds and herbivores may eat the capsules and so disperse the seed.

(5) Seed germination - Seed germinability is usually high, but germination itself is often highly erratic. Laboratory observations indicate a possible mechanism in that some viable seed only germinated after being soaked and dried. Such a mechanism to spread out germination over a long period is of obvious advantage to a species in which seedling establishment seems to be such a critical part of its life cycle.

There is evidence from the wild that germination does occur over a very long period, from early autumn as soon as the seed is shed, till at least the spring (April).

(6) Development from seedling to adult plant - A seedling first produces a rosette bearing rotund leaves from whose axils spring flowering stems and sometimes rhizomes. Rhizomes then arise adventitiously from the upper part of the tap root. The rhizomes often branch underground. On reaching the surface the rhizome apices either develop directly into flowering shoots, or, if they are less vigorous, produce rosettes which behave in the same way as the primary rosette formed by the seedling.

(7) The occurrence of seedlings in the wild - In the wild seedlings and young plants are rare, germination and survival of the young seedlings only being possible in continually moist microhabitats with a limited amount of competition. Once established in such a situation, colonisation of surrounding habitats quite unsuitable for seedling establishment is possible by vegetative spread. Such spread may in fact be necessary as the damp shady conditions suitable for seedling establishment are often quite unsuitable for the optimum development of the mature plant, which seems to prefer dry, sunny habitats.

Cliffs, where such dissimilar micro-habitats occur close together, thus provide a suitable habitat for C.rotundifolia. Even grassland can provide such conditions. Small bare batches of soil, produced by animal activity, are shaded and moist, and, as long as the grasses are not too large, the C.rotundifolia can produce stems which are at least as tall as the surrounding grasses, and the basal leaves can develop very long petioles.

(8) The genetic structure of topodemes - Observations suggest that young plants may be more vigorous than older established plants, and so may be capable of invading and perhaps replacing colonies of old plants.

CHAPTER 8 GEOGRAPHICAL DISTRIBUTION OF THE CYTODEMES IN THE BRITISH ISLES

SECTION 1 - INTRODUCTION

An examination of the distribution map of C.rotundifolia in the British Isles (Perring and Walters 1962) (fig. 1.3) reveals some peculiar features. It is rare in the lowland area round the Wash, in south-west England (Cornwall and Devon), in the North West Highlands of Scotland - especially away from the coast, and in the whole of Ireland. As C.rotundifolia is very easily recognised in flower, it is considered that its absence from these areas is real. Some under-recording is however likely especially in Ireland.

These gaps in the distribution have to be considered in the light of the fact that C.rotundifolia is characteristically a species of heathy grasslands and cliff ledges. These habitats offer a well-oxygenated substratum, a reasonably high light intensity, and often a relatively infertile soil.

Absence from the Wash area might therefore be due to the lack of suitable habitats, the whole area being intensively farmed and highly fertile. However this explanation could not possibly apply to the North West Highlands, or Ireland.

The climate of the south west differs from that of the rest of the British Isles in being warmer and milder. This does not lead to the exclusion of many species, and in fact results in the presence of a fair number of species which occur nowhere else in the British Isles (except perhaps in south west Ireland). That C.rotundifolia may not favour warm conditions is however, suggested by its restriction in northern Spain to cool damp gorges in the lowlands, and the higher reaches of the mountains. Also the wet acid soils of south west England are much less suitable for C.rotundifolia than the chalk and limestone grasslands of the neighbouring regions of southern England.

The North West Highlands do not differ markedly from the mountainous area south of the Great Glen, but their harder gneissose and quartzite rocks do tend

to give rise to poorer, more acid soils than the more rapidly weathering schistose rocks of the southern and central Highlands. The climate is also colder than that of the rest of Britain and the growing season shorter. This last factor in particular could impose serious restrictions on a late flowering species such as C.rotundifolia, and its restriction to coastal areas in the north-west could be interpreted as evidence in favour of this argument. Some species common throughout the rest of Great Britain are very rare in this area, but with such species as Mercurialis perennis the rarity of suitable sheltered calcareous habitats is probably an important factor. Certain species such as Arctous alpina are largely restricted to the North West Highlands, and their requirements seem to be for short cold summers to reduce competition.

In Ireland C.rotundifolia is quite common on the northern basaltic cliffs and in some such isolated limestone areas as the Burren and the Ben Bulbin area in Sligo. However its rarity throughout the rest of Ireland cannot be explained by any of the factors invoked to account for its absence from parts of Great Britain. The climatic and edaphic factors in Ireland seemed to be ideal, especially when the great extents of basaltic and limestone rocks is considered.

One of the main ways in which the Irish flora differs from that of Great Britain is in the absence of species which had not reached Ireland before it became an island. It was therefore considered possible that Irish C.rotundifolia might differ in some way from the British plants, and would thus be behaving as a separate entity with different ecological requirements. This suggestion was supported by Morisset's count of 2n=102 for a plant from the Galtee Mountains in County Tipperary, indicating that Irish plants might be hexaploid. However, three tetraploid counts reported by Böcher (1960) from Sligo and Donegal had to be considered.

Another remarkable gap in the distribution of C.rotundifolia is the Isle of Rhum. This absence was confirmed by the Nature Conservancy's Warden on the island, Mr. P. Wormwell, who has been looking out for the species for the last

eleven years. This gap in its distribution is surprising as C.rotundifolia is common on rocks of a similar, but less basic type, to those of Rhum in the neighbouring island of Mull and on the mainland in Ardnamurchan. It is also common on the machairs of the Outer Hebrides. A possible explanation is that the dispersal mechanism of the species is not efficient enough for it to be able to cross such wide sea barriers as it would have to cross to colonise Rhum.

Another interesting problem concerned the reported diploids in the eastern parts of England (Kovanda 1966b) which were likely to be contiguous, if not intermixed with tetraploids.

Very few counts were therefore available when the work for this thesis was begun (fig. 1.2), but those few suggested diploids in eastern England and perhaps Scotland, isolated occurrences of hexaploids in the south-west (C.rotundifolia is very rare in this region), and tetraploids throughout most of the country.

The counts reported here (table 4.2) presented a somewhat different picture (fig. 8.1). The detailed distributions of the cytodemes had therefore to be mapped out, and the areas where they were contiguous studied in detail. In this chapter I shall attempt to account for the distribution pattern found in Britain, dealing with each of the cytodemes in turn.

Pollen of Campanula (probably C.rotundifolia), and in one case seeds, have been reported intermittently since the last (Wiechselian) full glacial period (Godwin 1956, West 1970), so one or other cytodeme is a native plant of long standing, and this must be taken into account in considering present distributions.

SECTION 2 - THE SEARCH FOR DIPLOIDS

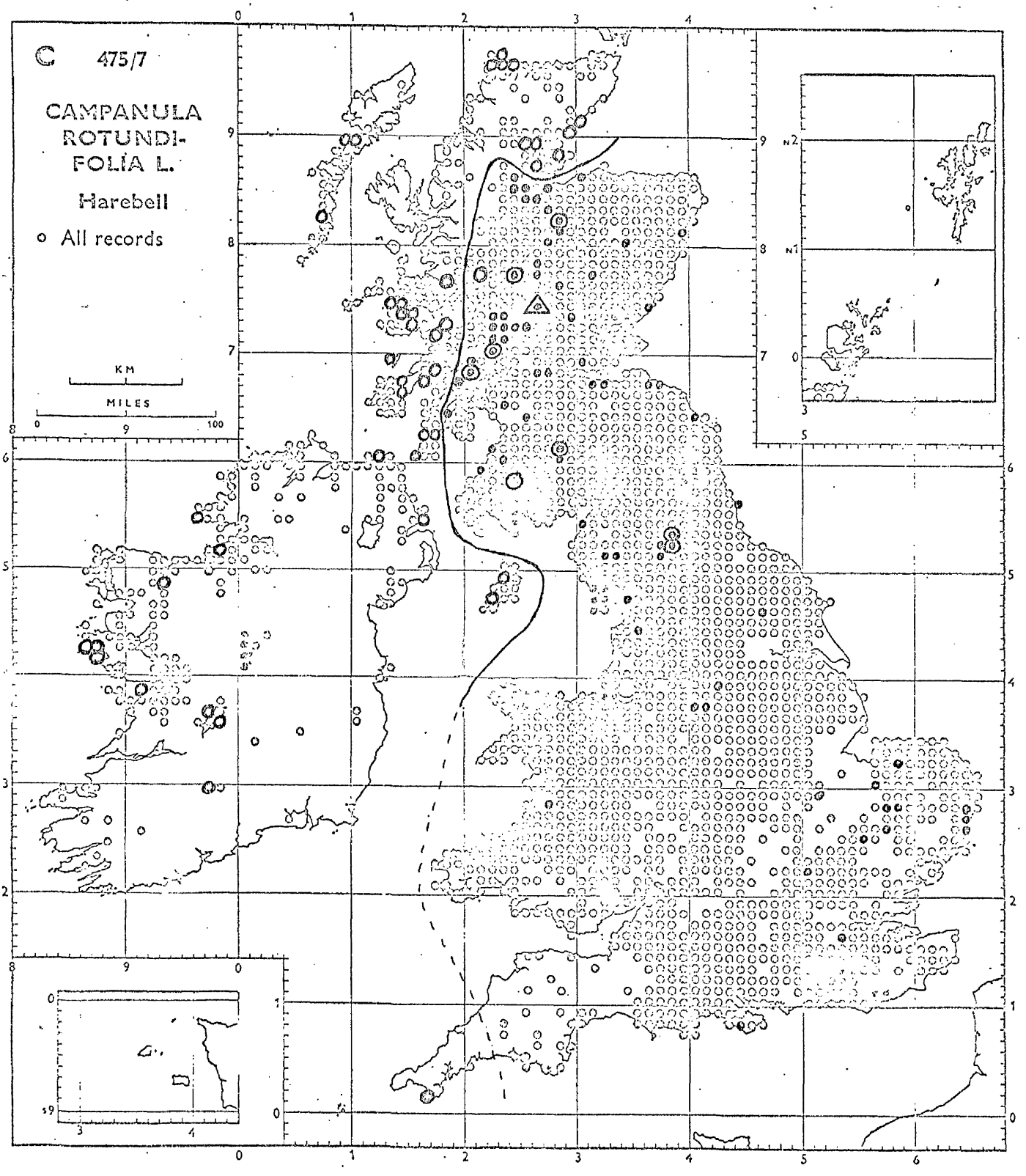
Kovanda's diploid counts have not been confirmed, despite the fact that seed and plants have been obtained from two of the exact locations from which

FIG. 8.1 The distribution of the tetraploid and hexaploid cytodemes of C.rotundifolia in the British Isles

• Tetraploid 2n = 68

O Hexaploid 2n = 102

△ Pentaploid 2n = 85



he obtained his seed, and from only a few hundred yards from the third station. This disagreement is sufficiently important to make it imperative to give the details of how Kovanda and I obtained our specimens.

(a) Fleam Dyke

Kovanda's material from Fleam Dyke, Cambridge, was a seed sample collected by Dr. D. Briggs in 1965. My collection consisted of 12 living plants and seed, also collected by Dr. D. Briggs from the same locality in 1967.

(b) Downham Market

The material from Downham Market, Norfolk, counted by Kovanda was again a seed sample, and was collected by Dr. P. Yeo of Cambridge in 1965. Dr. Yeo gave me the detailed grid reference and locality of his collection, and Dr. D. Butcher obtained seed and living plants from this locality for me. He reported that C.rotundifolia was rare in this area, and that the clone he sampled was the only one found in the locality.

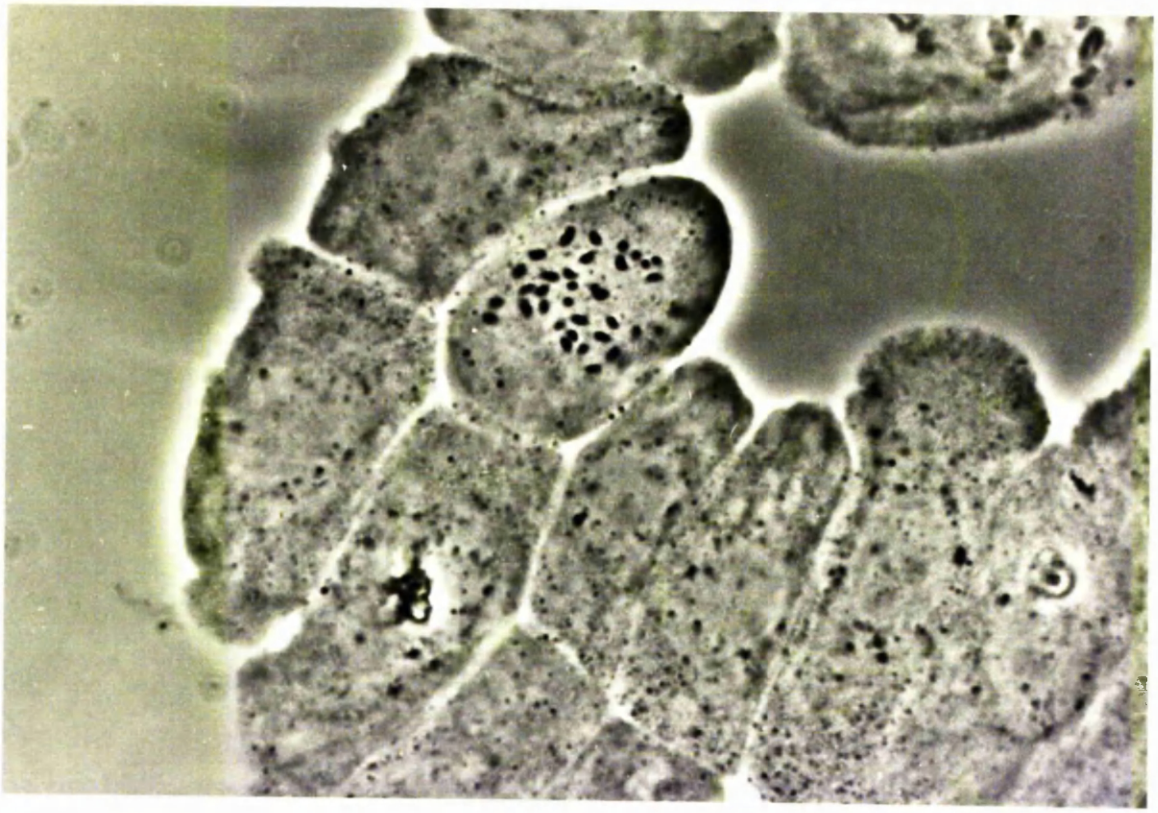
(c) Berwick

Kovanda's seed sample from Berwick was also collected by Dr. P. Yeo, and again I obtained details of the site, and collected material from a number of localities in the area.

All the specimens I obtained from the above three sites proved to be tetraploid.

On the basis of pollen grain measurements Böcher (1960) suggested that diploids might occur on the Isle of Wight. A seed sample from there, though giving plants with small flowered paniculate inflorescences and small pollen (fig. 5.27), proved to be tetraploid.

Although many specimens have been counted from such well known arctic-alpine refugia as Teesdale, Merrick, Ben Lawers, Ben Lui, The Cairnwell, Ben Nevis range, Ben Alder range, and Durness (C.rotundifolia is absent from Ben More Assynt and the Inchnadamph limestone), no arctic-montane diploids have been found.



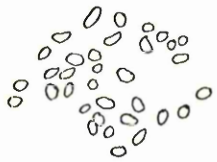


FIG. 8.2 Diploid cell in root of otherwise tetraploid plant.

Twice I have made apparently diploid counts on British plants, but further counts on the same plants proved them to be tetraploids. The diploid roots (which could not have belonged to another species as the pots held only C.rotundifolia) were rather thicker than normal and had only a small number of dividing cells. The chromosomes in these cells had a peculiar appearance (fig. 8.2) with the region round the centromere being contracted, but with the ends of the chromosome arms appearing very hazy and apparently uncontracted. Two such cells were seen in one root, and one in each of three other roots. These cells, and perhaps the whole roots, may have been the result of somatic reduction divisions, but this cannot be taken as proven.

I have therefore been unable to find diploids in the British Isles, but cannot rule out the possibility that they may be found - possibly on chalk in unglaciated areas of southern England south of the Thames and Severn valleys.

SECTION 3 - THE WIDESPREAD TETRAPLOID CYTODEME

By far the majority of harebells found throughout mainland Britain are tetraploid. Apart from scattered hexaploids, all harebells in the main island are tetraploid, except those in Cornwall, possibly Devon, and in a narrow coastal belt from Kintyre round the west, north and north east coasts of Scotland to Dingwall. The only large off-shore islands on which tetraploids occur are the Isle of Wight and Arran - nothing is known about C.rotundifolia in Anglesey. There are therefore few if any discontinuities in the distribution of the tetraploids, and just outwith their present range are habitats which seem highly suitable for colonisation, such as the Hebrides, limestone areas of north west Scotland, and especially Ireland. Some, but by no means all, of these habitats are occupied by the hexaploid cytodeme. However these areas are separated from the nearest plants of the tetraploid by stretches of either sea or bog, and long range seed dispersal is unlikely (Chapter 7). No species

mapped in either the Atlas of the British Flora (Perring and Walters 1962) or the Critical Supplement to the Atlas of the British Flora (Perring and Sell 1968) has the same distribution as that of tetraploid C.rotundifolia.

From the distribution of the tetraploid cytodeme it is suggested that it may be a relatively recent immigrant from the continent. We may suppose that it arrived after the land bridges to Ireland and the Hebrides had been broken by the rising sea level, and after north western coastal areas had been isolated by the development of forest or bog (West 1968, 1970).

The only results which would tend to argue against this theory are Böcher's report (1960) of tetraploids in north and west Ireland. As with Kovanda's diploid counts, I have tried very hard to confirm Böcher's results, obtaining 21 plants from one of his sites (Ben Bulbin, Sligo), and one from another (Slieve League, Donegal). The five plants counted from Ben Bulbin, and one from Donegal were hexaploid. His other site, Denegal coast, was too imprecise to be verified. My own plants from Slieve League and Ben Bulbin agree with Böcher's description of plants from these sites. All Irish plants proved to be hexaploid.

SECTION 4 - THE HEXAPLOID CYTODEME

If Böcher's report of tetraploids in Ireland can be discounted, hexaploids occur to the total exclusion of other cytodemes in Ireland, the Hebrides, the Isle of Man, and the west, north and north east Scottish coast from Campbelltown in Kintyre to Dingwall on the Cromarty Firth, north of Inverness. Hexaploid populations have also been found in 8 isolated localities within the distribution range of the tetraploids. Of these 8 isolated populations, five are in well recognised refugia of arctic-alpines: Teesdale; the Merrick, Kircudbrightshire; Ben an Lochain, Argyll; Ben Alder; and the Ben Nevis range. The other three are in more lowland stations - Wanlockhead, Lanarkshire; Glendaruel, Argyll; and Carrbridge, Inverness-shire.

(a) Main distribution area

Within the main distribution area of the hexaploids, in Cornwall, Ireland and the Isle of Man, and the Hebrides, they are obviously isolated from tetraploids. On the western coast of Scotland, on the other hand, the map (fig. 8.1) would suggest that the hexaploid populations are contiguous with tetraploid populations. In no locality, however, were such contiguous populations found. As one travels from east to west across the Scottish Highlands, especially in the north west, C.rotundifolia becomes less frequent. Eventually only the odd plant can be seen in a roadside verge, or on the well drained soil along stream banks. Finally, especially in the north west, there is a total absence of C.rotundifolia across great stretches of bog till one arrives at the west coast. Here C.rotundifolia, now as a hexaploid, can be found on basalt sea cliffs, sand dunes, and areas of limestone.

Within this area C.rotundifolia is sometimes very common, for example in the basalt cliffs of Northern Ireland, Mull, and Ardramurchan, and on the machairs and sand dunes of the Outer Hebrides. Elsewhere it can be quite rare, being confined to habitats which have not been forested since the last glaciation and often in association with arctic-alpines. At the Lizard it is confined to shady habitats, apparently being unable to colonise the sea cliff rock ledges or the Erica vagans heath, which become very hot and dry in summer. In the west of Ireland it is more or less confined to such well known refugia as the Burren and the shell sand areas of Connemara which support a small outpost of the Burren flora. It also grows in the well known localities for arctic-alpines on the cliffs of Muckanaght in Connemara and Ben Bulbin in Sligo. By Lough Conn it was found confined to moss tussocks in boulders on the lake shore with Galium boreale. These boulders are flooded in winter, and and the habitat is thus kept open and free from trees.

In the extreme north west of Scotland it is confined to such refugia as the Durness limestone, and the Bettyhill sand dunes. The hexaploid usually behaves as a calcicole, unable to stand much competition, and preferring a cool or cold climate. Also, in all the situations examined, its populations are separated from those of the tetraploid.

The distribution of the hexaploid cytodeme could be interpreted to be that of a species being replaced over most of its former range by a more vigorous new invader, the tetraploid. It therefore only inhabits those areas to which the invader has not yet spread.

(b) Isolated occurrences

Having considered the hexaploid within its main distribution range, we shall now consider the isolated hexaploid populations.

(i) Teesdale

In Teesdale the hexaploids grow on the limestone grassland with Gentiana verna on Widdybank Fell, and on the banks of the Tees down at least as far as High Force. On the Fell itself the limestone grassland communities are isolated by bog, unlike those on ~~the~~ Thistle Green on Cronkley Fell which are inhabited by tetraploids. These latter grasslands are contiguous with areas of upland grassland and Cronkley scar, both habitats suitable for colonisation by C.rotundifolia and via which the tetraploid could reach Thistle Green.

(ii) The Merrick, Kircudbrightshire

The hexaploid population on the Merrick is found on the summit plateaux in association with Salix herbacea in very open vegetation on solifluction terraces. Although only at an altitude of 810m (2700ft) it is probably the harshest environment in which I have found C.rotundifolia. The plateau merges downwards into upland grassland containing C.rotundifolia - probably the tetraploid cytodeme.

The one plant which survived from collections made on this mountain was the

most distinctive British specimen I have seen (fig. 5.24), with its open almost saucer shaped corolla, hemispherical ovary and single flowered stems. Taxonomically it is very close to the published descriptions of the most extreme form of C.gieseckiana.

(iii) Ben Alder

The situation on Ben Alder is similar to that on the Merrick, with the hexaploids occurring on the plateau and rock ledges at high altitudes 900-1050m (3000-3500ft) on the north western side of the mountain. Plateau plants were isolated from presumed tetraploids occurring on the lower slopes and in the Great South Coire (Garbh Coire). On the North East, East, South and West faces, the barrier was the very exposed rim of the plateau, while wet grassland and Vaccinium myrtillus - Empetrum hermaphroditum separate populations of the two cytodemes on the north west shoulder.

It is interesting to note that on Aonach Beag on the opposite side of the valley tetraploids were found on limestone at 990m (3300ft) in association with such rarities as Minuartia rubella and Veronica fruticans. However, unlike the isolated Ben Alder hexaploid topodeme, this topodeme was continuous down to Allt à Coire Mhoir to the valley over 390m (1300ft) below.

(iv) Ben Nevis

C.rotundifolia is very rare on Ben Nevis and neighbouring Aonach Beag, isolated individuals occurring in grassland and on rock ledges from 600-900m (2000-3000ft). Associated arctic-alpines included Saxifraga cernua, S.rivularis, Taraxacum craspedotum and Cystopteris montana. The two plants examined were hexaploids, and so presumably were the few other scattered plants seen. They bore few large flowers on relatively stout stems with hemispherical ovaries and corolla bases. In this valley at least, any upward spread from the lowlands in Glen Nevis (which might be inhabited by tetraploids) would be prevented by extensive Molinia-Myrica swamps.

(v) Ben an Lochain, near Arrochar, Argyll

Two hexaploid plants have been collected from Ben an Lochain, near Arrochar in Argyll. One specimen (75.7.A) was collected by a friend and its exact locality is unknown. The other (1.71.A) consisted of a few very weak non-flowering shoots growing among moss in a very shady crevice in a gully at about 810m (2700ft). This was by far the highest altitude at which I found C.rotundifolia on the south face of the mountain. As noted in the chapter on morphology, this plant, unlike tetraploids from lower down on the same mountain, had the hemispherical ovary, the rounded corolla base, and the large flowers of C.gieseckiana. I believe the other hexaploid sample to have come from a different clone as it differed morphologically in having as a constant character straight corolla lobes (fig. 5.23). On this mountain are to be found such arctic-alpines as Poa alpina, Saxifrage oppositifolia and viviparous Deschampsia caespitosa.

(vi) Ben Lawers

A most significant find was the discovery of two pentaploids on Ben Lawers. Their presence is taken as an indication of the current, or at least recent, occurrence of hexaploids on this famous mountain. Of 13 specimens collected from the highest reaches of the mountain only the two highest samples were pentaploid. These were collected on the West Rocks and the coire above Lochan nan Cat. All the other specimens proved to be tetraploid, and differed morphologically from the pentaploids in being smaller flowered (fig. 8.3). It is perhaps significant that the summit colonies of C.rotundifolia on Ben Lawers are not isolated from neighbouring lowland populations as they are on Ben Alder. The species is more or less continuously distributed in the grasslands, which extend from the valleys to the summit of the mountain. Therefore, unlike most of the previously described mountain stations of the hexaploids, the Ben Lawers topodeme has not been free from invasion by tetraploids.

FIG. 8.3 Slender tetraploids (on left) and more robust pentaploid (on right) from Ben Lawers (cultivated material).

It cannot be without significance that the mountain areas in which the hexaploids occur are some of the highest in Britain, and are often either plateaux, or have much ground above 900m (3000ft). They are also some of the most important refugia of arctic-alpines in Britain. Unfortunately no samples of C. rotundifolia have been obtained from Clova, Caenlochan, or the Cairngorms, but material from many less well known sites are tetraploid - The Cairnwell limestone, Ben Lui, Ben Dorain (Bridge of Orchy), The Glen Falloch Hills, the Braes of Balquhidder, and Sca Fell Pike. Harebells are absent from the well known mountain habitats of arctic-alpines in the North West Highlands - Inchnadamph, Ben More, Assynt, Seana Bhraigh and Beinn Dearg near Ullapool, Sgurr Mor Fannich, and An Teallach near Dundonnel in Wester Ross.

Although the occurrence of the hexaploid or pentaploid cytodeme in the above five localities gives a clear picture of it behaving as an arctic-alpine, there are also three other much more problematical occurrences; at Glendaruel, Argyll; Wanlockhead, Lanarkshire; and Carrbridge, Inverness-shire.

(vii) Glendaruel

In Glendaruel a small hexaploid population was found on stream banks in a river system largely surrounded by dense woodland in its lower parts. As Glendaruel is not far from the west coast area inhabited exclusively by hexaploids, this population may have been only recently isolated from the main distribution area of the hexaploids. It seems that the open habits along the stream banks enable the population to survive, while the surrounding woodlands protect it from invasion by the tetraploids. A plant from a neighbouring meadow was aneuploid with 2n=88 - this is only the second record of an aneuploid within the section Heterophylla (Böcher 1963).

(viii) Wanlockhead

Several hexaploid individuals, apparently of different genotype, have been obtained from a grassy pasture near Wanlockhead. Nothing further is known

about the site, or about the polyploid level of plants in the neighbouring hills. There are many arctic-alpines in the hills in this area, but the site at which the hexaploids were found was not a habitat in which one would expect to find arctic-alpines, and the plants themselves differed very little morphologically from the average of British tetraploids.

(ix) Carrbridge

The single hexaploid individual collected near Carrbridge, Inverness-shire, grew in an otherwise tetraploid population. It differed morphologically from these only in its rather short broad flower.

It is possible that the single hexaploid plant from Carrbridge, and perhaps those from Wanlockhead, have been derived from the neighbouring tetraploids through unreduced gametes. The lack of morphological features to distinguish between the hexaploids and tetraploids from each area supports this theory. The high frequency of giant pollen grains in some tetraploid populations (to 40% in 51.6.B) makes it quite likely that hexaploids could have arisen in this way.

A similar origin of hexaploids from tetraploids by means of unreduced gametes is described in Potentilla anserina by Rousi (1965), and Ockenden and Walters (1968). In this species all the hexaploids found occurred in otherwise tetraploid populations. They were almost totally sterile, and survived only through vegetative reproduction.

SECTION 5 - CONCLUDING REMARKS

My conclusions regarding the distribution of the cytodemes of C.rotundifolia in the British Isles are as follows:-

(a) The presence of lowland diploids is doubted. If they do occur the most likely place is eastern and southern Britain (in fact in the areas from which Kovanda reports them).

Whether we accept Kovanda's counts or not makes little difference to the interpretation being put forward to explain the distribution of the tetraploid and hexaploid cytodemes. There is no evidence that diploids related to those of Greenland, Spitzbergen, and North Norway, occur in the British Isles.

(b) Tetraploid populations are distributed more or less continuously throughout mainland Great Britain from the English Channel northwards to the Great Glen, with gaps in the South West, the Wash area, the North Highlands, and the Hebrides. This cytodeme is therefore probably a relatively recent (post-glacial) immigrant from the continent.

(c) Hexaploid populations are distributed in a very discontinous manner throughout Ireland and the western and northern seaboards of Great Britain. In these areas tetraploids are totally absent. Such a Lusitanian distribution pattern has been stated (West 1970) to be a relic distribution characteristic of species which have been present in the British Isles for a long time, and have probably persisted here through at least one glaciation.

Hexaploid topodemes also occur in isolated pockets within the distribution area of the tetraploids, usually, but not always, in mountain habitats in association with arctic-alpines.

A further discussion of the geographical distribution of cytodemes examining areas outside the British Isles appears in Chapter 11.

CHAPTER 9. HYBRIDISATION EXPERIMENTS

SECTION 1 - INTRODUCTION

Now that the morphology, ecology, and distribution of the several species and cytodemes studied have been dealt with, some consideration will be given to the possibility of gene exchange between these various entities. The techniques used in making the crosses have been described in Chapter 7.

A number of crossing experiments in the genus Campanula are reported in the literature. Gadella (1964, 1966) attempted many interspecific crosses, often between quite dissimilar species, in his attempt to find the most natural way of subdividing the genus. He also carried out some crosses between species within the subsection Heterophylla, and reported that C.cochleariifolia was not crossable with any of the three cytodemes of C.rotundifolia. Reciprocal crosses gave similar results. Bielawska (1964), however, reported limited interfertility between C.cochleariifolia and tetraploid C.rotundifolia, although less than half the progeny were the expected triploids, the majority being tetraploid. Crosses between lowland and montane genotypes of C.rotundifolia and between these and "C.polymorpha" and C.gelida (here named C.schcuchzeri) were also made (Bielawska 1968). No distinct breeding barriers were found between either the ecodemes or the species. Without giving any data, Böcher (1966) states that arctic and temperate diploids crossed "without any difficulty", as did tetraploids from both regions. He also successfully carried out crosses between diploids and tetraploids. Thus C.gieseckiana (arctic) and C.rotundifolia are presumably freely interfertile.

The plan of this chapter is as follows. Firstly gene exchange between tetraploid topodemes from within the British Isles will be discussed, and then British hexaploids will be considered in the same way. Following this, consideration of intracytodeme gene exchange between British topodemes, non-British topodemes of C.rotundifolia, and related species will be brought into the discussion.

Both intracytodeme and intercytodeme crosses involving diploids will then be dealt with. This will be followed by an account of crosses between tetraploids and hexaploids, and further crosses involving the resultant pentaploids.

Crosses involving C.arvatica, a species not belonging to the subsection Heterophylla, will be briefly mentioned.

The chapter will close with a short discussion on the significance of the results of the hybridisations to the evolution and taxonomy of C.rotundifolia and the species with which it was crossed.

In many of the crosses described below only an F_1 generation has been raised, time and space precluding the raising of further generations. It is realised that the ability to produce an F_1 does not necessarily indicate the ability of the parental entities to exchange genes - the F_1 might be infertile (Stebbins, 1958). The ease of production of an F_1 does however give some indication of the degree of interfertility. In some cases F_1 plants were successfully open pollinated, while in others they were backcrossed and an F_2 raised, and where this has been done a much better assessment of the degree of interfertility can be obtained.

SECTION 2 - CROSSES BETWEEN BRITISH TETRAPLOIDS (Table 9.1)

It can be seen from the table that 17 of the 27 crosses resulted in the production of good seed giving over 40% germination. Two other crosses gave good seed which was not tested for germinability, leaving 8 which either failed completely or had poor germination.

The 19 crosses which yielded quantities of fully developed seed can be considered to have been successful, but the other 8 will have to be examined carefully to see if there is any evidence of the existence of incompatibility barriers between topodemes from different parts of the British Isles.

Apart from cross (4), it is noticeable that four female parents are

TABLE 9.1 THE RESULTS OF CROSSES BETWEEN TETRAPLOIDS FROM THE BRITISH ISLES

Cross No.	Female parent Code No	Female parent Locality	Male parent Code No	Male parent Locality	Capsules +seed	Capsules -seed	Good seed	% Germination
1	41.6.A	Muir of Ord	38.6.F	Blair Atholl	5	4	+	83
2	41.6.A	Muir of Ord	64.6.B	Campsies	7	0	+	70
3	41.6.B	Muir of Ord	38.6.F	Blair Atholl	1	0	+	60
4	41.6.B	Muir of Ord	88.6.A	Ben Lui	0	2	0	0
5	41.6.C	Muir of Ord	64.6.B	Campsies	4	10	+	80
6	41.6.C	Muir of Ord	10.6.A	Tighnabruaich	1	2	+	48
7	69.8.A	Moy	64.6.B	Campsies	4	0	+	96
8	46.6.A	Aviemore	38.6.F	Blair Atholl	3	1	+	75
9	46.6.A	Aviemore	64.6.B	Campsies	2	1	thin +	18/∞
10	38.6.F	Blair Atholl	45.6.A	Carrbridge	0	2	0	0
11	38.6.F	Blair Atholl	88.6.A	Ben Lui	1	0	0	0
12	38.6.F	Blair Atholl	64.6.B	Campsies	9	9	+	-
13	38.6.F	Blair Atholl	10.6.A	Tighnabruaich	0	3	0	0
14	38.6.F	Blair Atholl	45.6.A	Carrbridge	2	1	+	91
15	44.7.A	Bridge of Orchy	1.7.B	Cambridge	3	0	-	-
16	89.6.C	Arrochar	38.6.F	Blair Atholl	2	0	+	89
17	89.6.C	Arrochar	64.6.B	Campsies	1	4	+	89
18	23.6.B	Glendaruel	46.6.A	Aviemore	0	2	0	0
19	23.6.B	Glendaruel	38.6.F	Blair Atholl	1	0	thin +	11
20	23.6.B	Glendaruel	64.6.B	Campsies	2	1	+	42
21	64.6.B	Campsies	41.6.B	Muir of Ord	3	4	+	53
22	64.6.B	Campsies	69.8.A	Moy	4	0	+	68
23	64.6.B	Campsies	38.6.F	Blair Atholl	5	0	+	42
24	65.6.E	Cramond	88.6.A	Ben Lui	3	6	+	79
25	65.6.E	Cramond	64.6.B	Campsies	8	5	+	77
26	10.6.A	Tighnabruaich	64.6.B	Campsies	1	0	thin +	1/∞
27	61.6.B	Girvan	64.6.B	Campsies	2	0	+	92

particularly associated with failure or poor germination in crosses. These four plants, from Aviemore, Blair Atholl, Glendaruel, and Tighnabruaich, are noteworthy in being the four most delicate plants used as female parents, having small flowers borne on very fine pedicels. The Glendaruel plant had in fact the smallest flowers of all the British specimens seen, though in this it was not typical of the rest of the Glendaruel topodeme. Having small floral parts made the flowers of these plants more susceptible to damage of all sorts, especially that caused by red spider. In crosses, 9, 11, 19, and 26 the capsules were so badly attacked that they dried up prematurely and the seed was not properly formed. Also, in none of these 8 crosses was more than three flowers pollinated, so that the degree of replication was inadequate for a negative result to be highly significant.

Despite these possible technical reasons for the failure of some crosses, it is worth while examining the results to see if any pattern emerges. For example it would be of interest if the plants which failed as female parents also failed as pollen parents. It is true that the Blair Atholl and Tighnabruaich plants failed or did badly as male parents in crosses 13 and 19, but they performed successfully in crosses 1, 3, 8, 16 and 23, and 6 respectively. The Ben Lui plant, which was not used as a female parent, performed badly as a male parent in two crosses (4, 11), but a third cross (24) was highly successful.

Thus, no plant consistently failed or performed badly in all crosses involving it, and there is no need to implicate genetic factors as a cause of any of the failures, obvious technical factors offering a reasonable explanation in all cases. On the other hand the possibility of some cross-incompatibility cannot be ruled out. The Glendaruel plant came from a relatively toxic serpentine soil, and three crosses involving it were relatively unsuccessful, and Antonovics et al (1971) have pointed out the evolutionary advantage of topodemes tolerant to heavy metals evolving incompatibility with intolerant genotypes.

Although all the tetraploids used in the above crosses are of Scottish origin, they were chosen to be as morphologically diverse as possible. It was unfortunately not possible to repeat most of the crosses which gave negative results due to the death of one or other of the parents.

SECTION 3 - CROSSES BETWEEN BRITISH HEXAPLOIDS (Table 9.2)

The hexaploid plants used in these crosses include the most northerly (Durness) and most southerly (Lizard) plants collected within the British Isles. Plants from isolated stations as well as some from the main distribution area are included.

All the crosses made were successful, though a high proportion of apparently viable dormant seed was left after two of the germination tests. It is, therefore, concluded that there are unlikely to be breeding barriers between hexaploid topodemes from even the most widely separated parts of the British Isles.

SECTION 4 - TETRAPLOID-TETRAPLOID CROSSES INVOLVING NON-BRITISH TETRAPLOIDS (Table 9.3)

C. rotundifolia x C. gieseckiana (Iceland) Böcher (1966), working with material of C. gieseckiana from Greenland, reports these two species to be completely interfertile at the tetraploid level. The single cross I have made using an Icelandic plant is in agreement with this result.

C. rotundifolia x C. asturica Four of the five crosses were wholly successful, all capsules in which the pollination succeeded producing a normal number of fully developed seed. The fact that the seed from the only sample which was germinated only gave 6.5% germination is considered to be relatively unimportant as all the ungerminated seeds were fully developed and the low percentage germination is interpreted as being the result of dormancy. The

TABLE 9.2 THE RESULTS OF CROSSES BETWEEN HEXAPLOIDS

Female parent Code No.	Locality	Male Parent Code No.	Locality	Capsules +seed	Capsules -seed	Good seed	% Germination
76.8.C	Durness	83.8.D	Widdybank	2	1	+	96
76.8.C	Durness	92.6.A	Lizard	6	4	+	-
45.6.B	Carrbridge	61.6.E	Strontian	2	0	+	96
1.6.A	Oban	2.6.A	Oban	1	1	+	51
75.7.A	Arrochar	76.8.C	Durness	1	0	+	50
101.6.G	Isle of Man	45.6.B	Carrbridge	5	0	+	100
20.8.C	Pontoon, Co. Mayo	83.8.D	Widdybank	1	0	+	-
16.8.A	Connemara	76.8.C	Durness	1	2	+	-

TABLE 9.3 THE RESULTS OF TETRAPLOID x TETRAPLOID CROSSES INVOLVING NON-BRITISH TETRAPLOIDS

Female Parent Species	Locality	Male Parent Species	Locality	Capsules +seed	Capsules -seed	Good seed	% Germination
C.rotundifolia	Scotland	C. gieseckiana	E.Iceland	8	1	+	-
C.rotundifolia	Scotland	C.asturica	N.Spain	0	10	0	0
C.rotundifolia	Scotland	C.asturica	N.Spain	6	11	+	-
C.asturica	N.Spain	C.rotundifolia	Scotland	14	0	+	-
C.asturica	N.Spain	C.rotundifolia	Scotland	4	0	+	-
C.asturica	N.Spain	C.rotundifolia	Scotland	5	0	+	6.5
C.rotundifolia	Scotland	C.ficarioides	N.Spain	1	0	+	55
C.rotundifolia	Scotland	C.ficarioides	N.Spain	2	5	+	50
C.ficarioides	N.Spain	C.rotundifolia	Scotland	5	0	+	50
C.rotundifolia	Scotland	C.scheuchzeri	Austria	1	2	+	44
C.rotundifolia	Scotland	C.scheuchzeri	Austria	1	2	+	78
C.scheuchzeri	Austria	C.rotundifolia	Scotland	0	12	0	0
C.scheuchzeri	Austria	C.rotundifolia	Scotland	6	6	+	31
C.gieseckiana	E.Iceland	C.intercedens	Lake Superior	37	0	+	-
C.intercedens	Lake Superior	C.gieseckiana	E.Iceland	1	2	thin	-

fact that ten flowers were pollinated in the cross which proved unsuccessful suggests that the failure might be significant, with the possibility that though some genotypes of both species are intercrossable, others may not be. On the other hand, the reciprocal cross yielded fourteen capsules each containing a normal quantity of seed.

It is probable that C.rotundifolia and C.asturica are interfertile, but there is some indication that this may not extend to all genotypes.

C.rotundifolia x C.ficarioides All three crosses involving these two species were highly successful, yielding capsules containing a normal number of fully developed seed. The percentage germination figures are perhaps rather low, but seeds of C.ficarioides are highly dormant.

It is perhaps worth noting that C.ficarioides is probably ecologically isolated from neighbouring topodemes of tetraploid relatives of C.rotundifolia in north Spain (C.asturica). C.ficarioides was only found on shale, whereas C.asturica appears to be confined to limestone.

C.rotundifolia x C.scheuchzeri As in the case of crosses between C.rotundifolia and C.asturica, though most of the crosses were highly successful, one failed completely. However the female parent in this case was C.scheuchzeri, and in the other cross in which it was the female parent the seed showed a relatively low percentage germination.

This may suggest a certain degree of cross-incompatibility between these two species. On the other hand, very little of the seed produced was not well developed, and the relatively hairy C.scheuchzeri plants suffered badly from red spider attack.

Bielawska (1968) reports Polish material of these two species to be more or less wholly interfertile, but Kovanda (1968 and pers. comm.) believes the material named C.scheuchzeri by Bielawska to belong to a separate species C.gelida.

C.gieseckiana (Iceland) x C.intercedens This cross succeeded in one direction only, but the flowering stem of the C.intercedens plant used as a female parent died prematurely of an unknown cause. The production of thin poorly developed seed by this plant was probably a result of this fact.

These two plants are probably wholly interfertile.

Summary of tetraploid x tetraploid crosses involving non-British plants.

From the results discussed above I do not believe that there is any definite evidence of sterility barriers operating at the level of primary crosses between the tetraploids used in the crosses. This is the case despite the fact that the plants came from Europe, Iceland, and America, and some of them belong to species (C.scheuchzeri and C.ficarioides) which are quite morphologically distinct from C.rotundifolia.

SECTION 5 - HEXAPLOID - HEXAPLOID CROSSES INVOLVING NON-BRITISH HEXAPLOIDS

(Table 9.4)

C.rotundifolia x C.rotundifolia. These crosses were made between one of the two Spanish hexaploids and several Scottish and Irish plants. The results were rather variable. All but the one cross which failed completely resulted in capsules full of seed, but one of these had a low percentage germination (26%). Another, though having fully developed seed and a high percentage germination (84%), resulted in seedlings which developed hardly any roots. It is perhaps worthy of note that the cross giving seedlings with poor root development and that giving only 26% germination are reciprocal crosses.

It is therefore concluded that the results of crossing the Spanish hexaploid with British hexaploids varies with the genotypes used. A low degree of cross-incompatibility seems to be present.

TABLE 9.4 THE RESULTS OF HEXAPLOID x HEXAPLOID CROSSES INVOLVING NON-BRITISH HEXAPLOIDS

Female parent		Male Parent		Capsules		Good seed	% Germination
Species	Locality	Species	Locality	+seed	-seed		
C.rotundifolia	Scotland	C.rotundifolia	N.Spain	4	6	+	57
C.rotundifolia	Scotland	C.rotundifolia	N.Spain	3	0	+	84
C.rotundifolia	Ireland	C.rotundifolia	N.Spain	1	0	+	very poor root growth 84
C.rotundifolia	Ireland	C.rotundifolia	N.Spain	1	0	+	55
C.rotundifolia	N.Spain	C.rotundifolia	Scotland	9	0	+	91
C.rotundifolia	N.Spain	C.rotundifolia	Scotland	0	6	0	0
C.rotundifolia	N.Spain	C.rotundifolia	Ireland	3	4	+	26
C.rotundifolia	Scotland	C.latisepal	Alaska	1	2	thin 0	0
C.latisepal	Alaska	C.rotundifolia	Scotland	2	3	thin 0	0
C.latisepal	Alaska	C.rotundifolia	Ireland	1	4	thin 0	-
C.latisepal	Alaska	C. ieseckiana	Canada	4	0	+	+

C.rotundifolia x C.latisepala. In the three crosses made at least one capsule in each cross swelled and produced a full crop of seed. However, all but two seeds in one cross were thin and not fully formed. C.latisepala is therefore virtually incapable of crossing with hexaploids from the British Isles.

C.latisepala x C.gieseckiana (Canada). In contrast to the result obtained with British hexaploids, the Canadian hexaploid appears to be freely crossable with Alaskan C.latisepala. It is very unfortunate that it has not yet been possible to cross the Canadian plant with British hexaploids.

Summary of hexaploid-hexaploid crosses involving non-British plants

Breeding barriers appear to be found between hexaploid topodemes from widely distant sources. There is a low degree of incompatibility between the Spanish and British plants, and the Alaskan C.latisepala seems to be virtually reproductively isolated from British genotypes. This result is perhaps rather surprising as there seem to be no such barriers at the tetraploid level. On the other hand, the facts reported here are positive evidence in favour of the hypothesis put forward in Chapters 8 and 11 that the hexaploids are a relict type of more ancient origin than most of the common tetraploids.

SECTION 6 - CROSSES INVOLVING DIPLOIDS (Table 9.5)

As only three diploid plants were used in these crosses, one specimen each of C.rotundifolia, C.gieseckiana and C.cochlearifolia, all the hybridisations in which they were involved will be discussed together.

Diploid x diploid. Two of the three possible crosses involving the three species were made, and all three yielded capsules full of seed. The low germination obtained from seed borne on the C.rotundifolia plant is not believed to be significant as all the seed were fully formed. Seed of this plant showed a strong dormancy which could only be broken by several wetting-drying cycles,

TABLE 9.5

THE RESULTS OF CROSSES INVOLVING NON-BRITISH DIPLOIDS

Female Parent			Male Parent			Capsules		Good seed	Percentage germination
2n	Species	Locality	2n	Species	Locality	+seed	-seed		
(A) Diploid x diploid									
2x	C.rotundifolia	E.Germany	2x	C.gieseckiana	Greenland	6	0	+	$\frac{9}{68}$ many variegated
2x	C.gieseckiana	Greenland	2x	C.rotundifolia	E.Germany	8	0	+ thin	69 chlorotic
2x	C.cochleariifolia	Austria	2x	C.rotundifolia	E.Germany	48	0	+	74
(B) Diploid x tetraploid									
2x	C.rotundifolia	E.Germany	4x	C.rotundifolia	Scotland	12	0	0	0
4x	C.rotundifolia	Scotland	2x	C.rotundifolia	E.Germany	0	3	0	0
4x	"	"	2x	"	"	4	0	thin $\frac{2}{88}$	0
4x	"	"	2x	"	"	6	1	thin $\frac{2}{88}$	0
4x	C.rotundifolia	Scotland	2x	C.gieseckiana	Greenland	3	0	thin +	1 $(\frac{1}{81})$
4x	"	"	2x	"	"	6	0	thin $\frac{2}{88}$	0
2x	C.gieseckiana	Greenland	4x	C.gieseckiana	E.Iceland	6	0	0	0
4x	C.gieseckiana	E.Iceland	2x	C.gieseckiana	Greenland	15	1	0	0
4x	"	E.Iceland	2x	"	Greenland	24	4	thin +	$\frac{20}{88}$
2x	C.cochleariifolia	Austria	4x	C.rotundifolia	Scotland	11	0	0	0
(C) Diploid x hexaploid									
2x	C.rotundifolia	E.Germany	6x	C.rotundifolia	Scotland	9	1	0	0
2x	"	"	6x	"	"	6	0	0	0
6x	C.rotundifolia	Scotland	2x	C.rotundifolia	E.Germany	0	6	0	0
6x	"	"	2x	"	"	10	0	0	0
6x	"	"	2x	"	"	0	3	0	0
6x	"	N.Spain	2x	"	"	0	9	0	0
2x	C.gieseckiana	Greenland	6x	C.rotundifolia	Scotland	7	0	0	0
6x	C.rotundifolia	Scotland	2x	C.gieseckiana	Greenland	14	4	0	0
6x	"	"	2x	"	"	0	3	0	0

and the figure given is the result of only one wetting.

The cross C.gieseckiana x C.rotundifolia yielded many vigorous offspring about 5% of which were variegated, having yellow chlorphyll-less segments in their leaves.

Although the cross C.cochleariifolia x C.rotundifolia appears highly successful on the basis of the figures given, all the seedlings were highly chlorotic and had poor root development. Only one survived to maturity, and it proved to be diploid (fig. 10.3).

Diploid C.rotundifolia and diploid C.gieseckiana therefore appear to have a certain degree of interfertility. This conclusion agrees with that of Böcher (1966). On the other hand a strong barrier of hybrid inviability separates diploid C.rotundifolia and C.cochleariifolia.

Diploid x tetraploid.

Intercytodeme crosses involving C.rotundifolia and C.gieseckiana had only a very limited success. Most of the crosses resulted in the development of many capsules full of seed, but in every case by far the majority of the seed was thin and inviable. As these crosses have only been performed this year, the progenies are still very young and their chromosome numbers are unknown. It is anticipated that many will be triploid, though a proportion of tetraploids resulting from unreduced gametes is to be expected (cf. Bielawska 1964, 1969). As in the case of Bielawska's (1964) crosses with C.cochleariifolia seed was only produced when the female parent was the tetraploid C.rotundifolia. The failure of the cross C.cochleariifolia ♀ x C.rotundifolia ♂ is, therefore in agreement with Bielawska's results. Bielawska's successful cross, tetraploid C.rotundifolia ♀ x C.cochleariifolia ♂ could not be repeated using my material as my single speciment of C.cochleariifolia was pollen sterile in cultivation.

Diploid x hexaploid

Though many capsules developed normally after diploid x hexaploid cross-pollinations, no fully developed or viable seed was produced. Only Gadella (1964) has obtained viable seed from such crosses, but the seedlings died at an early stage.

SECTION 7 - TETRAPLOID-HEXAPLOID CROSSES (Table 9.6)

Quite a number of these crosses were fairly successful, yielding pentaploid offspring. However, one facet of all these crosses which does not show in the table is that capsules containing the hybrid seed always had a high proportion of thin shrunken seeds of all sizes.

The pentaploid progenies showed no obvious lack of vigour and some individuals produced pollen, although always in reduced quantities. Gadella (1964) similarly obtained pentaploids with both tetraploids and hexaploids as female parent, but he states that all his pentaploids lacked pollen.

SECTION 8 - CROSSES INVOLVING PENTAPLOIDS (Table 9.7)

Artificially produced pentaploids were backcrossed to both parents, some crosses succeeding in each direction. They were also selfed and crossed with other pentaploids, and again some of each type of pollination yielded seed.

In the backcrosses to tetraploids the F_2 plants had intermediate chromosome numbers (2n = 71-77), and intermediate numbers were also found in backcrosses to the hexaploid parent. This suggests that at meiosis in the pentaploids (at least in the cells giving rise to the functioning gametes) about 34 bivalents separate more or less regularly and the remaining univalents irregularly. Unlike the situation described by Bielawska (1964) in triploid-tetraploid backcrosses, there is no tendancy for the F_2 progeny to approach an even polyploid level parent in chromosome number.

The F_2 plants showed little or no reduction in vigour when compared with the parents. They were highly variably morphologically, and in pollen production. Some bore no pollen at all while others showed little reduction from the normal pollen yield of an euploid plant. Further study, especially of the meiosis, of these pentaploids and aneuploids is obviously necessary.

TABLE 9.6

THE RESULTS OF CROSSES BETWEEN TETRAPLOIDS AND HEXAPLOIDS

(A) Between plants from within the British Isles

Female Parent			Male Parent			Capsules		Percentage germination	Progeny 2n
Code No.	2n	Locality	Code No.	2n	Locality	+seed	-seed		
41.6.B	4x	Muir of Ord	45.6.B	6x	Carrbridge	2	0	1	-
46.6.A	4x	Aviemore	45.6.B	6x	"	0	2	0	-
38.6.F	4x	Blair Atholl	45.6.B	6x	"	4	5	11	-
51.6.B	4x	Girvan	93.6.A	6x	Tipperary	0	2	0	-
61.6.E	6x	Strontian	88.6.A	4x	Ben Lui	4	1	0	-
45.6.B	6x	Carrbridge	41.6.C	4x	Muir of Ord	2	1	1	-
45.6.B	6x	"	88.6.A	4x	Ben Lui	0	3	0	-
91.8.B	6x	Mull	64.6.B	4x	Campsies	1	6	3	- pollen
1.6.A	6x	Oban	45.6.A	4x	Carrbridge	2	0	50	5x pollen
1.6.A	6x	"	38.6.F	4x	Blair Atholl	2	1	23	5x pollen
1.6.A	6x	"	64.6.B	4x	Campsies	3	0	9	5x
2.6.A	6x	"	64.6.B	4x	"	1	6	1	-
101.6.G	6x	Isle of Man	41.6.C	4x	Muir of Ord	2	0	94	5x nopolle
101.6.G	6x	" "	10.6.A	4x	Tichnabruaich	4	0	44	5x

(B) Crosses between a British tetraploid and the Canadian hexaploid C.gieseckiana

Female Parent			Male Parent					Percentage germination	Progeny 2n
Code No.	2n	Locality	Code No.	2n	Locality	+seed	-seed		
64.6.B	4x	Campsies	97.6.S	6x	Canada	4	7	95	5x pollen
97.6.A	6x	Canada	64.6.B	4x	Campsies	7	1	0	-
97.6.S	6x	"	64.6.B	4x	"	18	12	2	-

TABLE 9.7

THE RESULTS OF CROSSES INVOLVING PENTAPLOIDS

Female Parent 2n	Male Parent 2n	Capsules +seed	Capsules -seed	Percentage germination	Progeny 2n
4x 64.6.B Campsies	5x Oban x Campsies 1	4	1	88	seedling had no roots
4x 64.6.B "	5x Oban x Campsies 2	6	9	78	71(2), 72-3, 73, 77.
4x 51.6.B Girvan	5x Oban x Campsies 2	5	1	98	"
5x Oban x Campsies 2	4x 64.6.B Campsies	5	0	45	75(2)
5x Oban x Campsies 1	Selfed	0	4	0	
5x Oban x Campsies 2	Selfed	1	7	38($\frac{8}{21}$)	seedlings had no roots
5x Oban x Campsies 1	5x Oban x Campsies 2	4	2	29	"
5x Oban x Campsies 2	5x Oban x Campsies 1	8	4	65	"
5x Isle of Man x Tighnabruaich	5x Oban x Campsies 1	0	18	0	0
5x Oban x Campsies	6x 1.6.A Oban	15	2	29	c90
5x Isle of Man x Tighnabruaich	6x 101.6.G Isle of Man	0	4	0	0
6x 91.8.B Mull	5x Oban x Campsies 2	3	0	3($\frac{1}{29}$)	"
6x 1.6.A Oban	5x Oban x Campsies 2	13	0	30	c90

SECTION 9 - CROSSES INVOLVING C.ARVATICA (Table 9.8)

C.arvatica (2n=28) is an endemic species in the mountains of northern Spain. Its systematic position in the genus is somewhat in doubt (Gadella 1966). It is not related to any other species of the x = 7 series except C.adsurgens with which it shares its isolated position. Gadella (l.c) places it in his Group VII (see table 3.4) with species having x = 17, but also 2n=30, and 32. It is thus placed in the same group as the subsection Heterophylla.

In crosses involving C.arvatica I have obtained at least poorly developed seed from all combinations tried except those involving C.asturica - the only species with which C.arvatica would naturally come into contact. The only crosses from which viable seed was obtained were those involving diploids of the C.rotundifolia group. However the seedlings were weak and none survived. Crook (1951) reports C.rotundifolia x C.arvatica hybrids in horticultural use.

SECTION 10 - SUMMARY OF RESULTS OF HYBRIDISATIONS

Plants from the British Isles

No breeding barriers have been proven to exist within the tetraploid and hexaploid topodemes within the British Isles. There are slight indications that such barriers might exist at the tetraploid level, but hexaploids from even the most widely separated localities are fully interfertile.

Diploids

As reported by Böcher (1966), diploid C.rotundifolia and diploid C.gieseckiana are almost wholly interfertile.

Diploid C.rotundifolia and C.cochleariifolia are intercrossable, but the offspring are very weak.

Tetraploids

No indication of any major breeding barrier has been found between any of the tetraploid taxa crossed - C.rotundifolia (Britain), C.gieseckiana (Iceland),

TABLE 9.8

THE RESULTS OF CROSSES INVOLVING C.ARVATICA (2n = 28)

Female Parent			Male Parent			Capsules		Good seed	Percentage germination
2n	Species	Locality	2n	Species	Locality	+seed	-seed		
34	C.rotundifolia	E.Germany	28	C.arvatica	N.Spain	4	0	+	6/33
34	C.cochlearifolia	Austria	28	"	"	7	0	+	17/33
68	C.rotundifolia	Campsies	28	"	"	2	6	0	0
68	C.asturica	N.Spain	28	"	"	0	12	0	0
68	"	"	28	"	"	0	2	0	0
28	C.arvatica	N.Spain	68	C.rotundifolia	Campsies	7	1	0	0

C.intercedens (N.America), C.asturica (N.Spain), C.scheuchzeri (Austria), and C.ficarioides (N.Spain).

Hexaploids

Barriers to crossing appear to exist between a north Spanish hexaploid and at least one hexaploid from the British Isles. Other genotypes are freely intercrossable.

British hexaploids and Alaskan C.latisepala are almost totally reproductively isolated. On the other hand C.latisepala is crossable with an east Canadian hexaploid.

Inter-cytodeme crosses

Offspring have been obtained from diploid x tetraploid and tetraploid x hexaploid crosses. Diploid x hexaploid crosses failed completely. The diploid x tetraploid progeny are still immature, but the pentaploid hybrids from the tetraploid x hexaploid crosses have reached maturity and yielded F_2 offspring.

C.arvatica

This species is crossable with considerable difficulty with diploid C.rotundifolia and C.cochleariifolia.

Although these different species and cytodemes are crossable in cultivation, this does not necessarily imply that they could hybridise in the wild. Many are separated by such great distances that they will never meet, and where they are sympatric they might be kept apart by ecological or pollinator specialisation. Also breeding barriers may evolve only where two species meet (Ingram 1968).

SECTION 11 - DISCUSSION

C.arvatica (2n=28)

Gadella's (1966) suggestion that C.arvatica belongs to his Group VII is

supported by its intercrossability with members of the Heterophylla. It is, however, only distantly related to the Heterophylla, having 2n=28.

C.cochleariifolia (2n=34)

Strong breeding barriers appear to exist between C.cochleariifolia and C.rotundifolia, though hybrids have been obtained from crosses with both diploid (this chapter) and tetraploid (Bielawska 1964) strains of C.rotundifolia. There are no reports in the literature of natural hybrids occurring, though Bielawska's studies have shown that they might be very difficult to detect. She has demonstrated that more than 50% of the hybrids obtained from the diploid x tetraploid cross were tetraploid, resulting from unreduced C.cochleariifolia pollen, and fully interfertile with tetraploids. Even triploid hybrids on crossing with tetraploid C.rotundifolia, gave rise to F_2 progenies with chromosome numbers approaching that of the tetraploids. Thus C.cochleariifolia could contribute genes to the gene-pool of C.rotundifolia without itself being contaminated by C.rotundifolia genes. Such a one-way gene traffic could increase the variability of C.rotundifolia without affecting the purity of C.cochleariifolia. However, no evidence has yet been obtained to suggest that such a process occurs in the wild.

The C.rotundifolia plant used in my cross was a lowland plant from East Germany. Diploids of C.rotundifolia do, however, occur in the Alps (Böcher 1960), and if these, like the lowland plant, are crossable with C.cochleariifolia, gene transfer from C.rotundifolia to C.cochleariifolia would be possible.

Despite the theoretical possibilities of gene exchange discussed above, the two species remain distinct. Hybrid inviability (in the case of the diploids) and perhaps ecological factors (in the Alps C.cochleariifolia is a scree plant while C.rotundifolia is a meadow plant) serve to keep them apart, and massive introgression is unlikely.

C.scheuchzeri (2n=68) and C.ficarioides (2n=68)

Plants of these two species are more or less freely interfertile with tetraploid British C.rotundifolia. It would be very interesting to know if they were equally interfertile with neighbouring strains of related tetraploids - C.rotundifolia in the case of C.scheuchzeri, and C.asturica for C.ficarioides. As mentioned earlier C.ficarioides and C.asturica are probably isolated ecologically, and the same may apply to C.scheuchzeri and C.rotundifolia, C.scheuchzeri occurring at higher altitudes, alpine specimens of C.rotundifolia taken from areas in which C.scheuchzeri is found, show no signs of introgression with that species. These two species, therefore appear to remain distinct, though I have no knowledge of C.scheuchzeri in the wild to enable me tomake a personal judgement. This conclusion is in line with recent taxonomic thought, and differs from the views of some earlier workers (e.g. Turesson 1925) who considered C.scheuchzeri to be an alpine ecodeme of C.rotundifolia.

C.rotundifolia and other members of the series Vulgares (C.gieseckiana, C.intercedens, and C.latisepala)

Previous reports (Böcher 1966) describe C.gieseckiana (diploid and tetraploid) and C.intercedens (tetraploid) as being freely crossable with C.rotundifolia plants of the same polyploid level. The results of the few crosses I have made are in line with these conclusions. Such interbreeding suggests little genome differentiation. Genome analysis of inter-cytodeme crosses would, therefore, not be expected to yield much information concerning chromosome homologies (cf. Manton 1934 and 1937 on Biscutella laevigata). Intercytodeme crosses were however made to study their interfertility as it was possible that gene transfer could occur between cytodemes in the way described by Bielawska for C.cochleariifolia and C.rotundifolia.

In diploid x tetraploid crosses involving a diploid C.rotundifolia plant no progeny were obtained. When a diploid plant of C.gieseckiana was used a small number of offspring were obtained from some crosses. Little comment can be made

on the significance of this result until the chromosome numbers of the progeny are known. On the other hand, it is clear that diploids and tetraploids are only crossable with difficulty and triploids are unlikely to be of great significance in the future evolution of the species complex. It is possible that in the past the creation of triploids from diploids through unreduced gametes was an essential step in the evolution of tetraploids.

In the complex, triploids have only once been reported in the wild (Kovanda 1966a), though Bielawska (1964), Gadella (1964), and Böcher (1966) have all produced them in cultivation. It is not possible to tell whether Gadella was dealing with C.rotundifolia s.s. as he was including in C.rotundifolia several of what Kovanda (1970c) now considers separate species. All his progeny died at an early stage. Böcher was working with plants from Europe, Greenland and America, and so presumably with C.rotundifolia, C.gieseckiana and C.intercedens but he makes no comments on any features of the progeny.

All my diploid x hexaploid crosses were unsuccessful. Although Gadella (l.c) reports that he obtained seed from such a cross, the offspring died at an early stage.

Like Gadella (l.c) I successfully obtained pentaploid offspring from tetraploid x hexaploid crosses. However, all Gadella's pentaploids were pollen sterile whereas some of mine produced quantities of pollen. I backcrossed one of the pentaploids to both parents to see if there was any tendancy for the F_2 generation to approach euploid chromosome numbers. If this had been the case it could have meant that pentaploids might have mediated gene transfer between tetraploids and hexaploids in the same way that triploids could between C.cochleariifolia and C.rotundifolia (Bielawska 1964). F_2 chromosome numbers intermediate between those of the parents were found, so the possibility of such gene transfer seems remote.

As hexaploids are most likely to have arisen as a result of non-reduction or chromosome doubling in a triploid, or through non-reduction in a tetraploid,

pentaploids are unlikely to have had any evolutionary significance.

Pentaploids had not been reported from the wild until they were found on Ben Lawers (Chapter 4). As has already been mentioned (Chapter 7), the occurrence of pentaploids in the apparent absence of hexaploids indicates the former presence of hexaploids in this locality.

As mentioned above, aneuploids can easily be produced by crossing tetraploids and hexaploids with the pentaploids. A plant with 2n=88, probably resulting from a pentaploid × hexaploid cross, has been discovered in the wild (Chapter 4). A strange plant with 2n=74+4B reported from France by Böcher (1963) is possibly an offspring from a pentaploid × tetraploid cross which has had both C.rotundifolia and C.scheuchzeri in its ancestry.

Pentaploids are probably of little significance in evolution, but the ease with which they are produced may severly limit the reproductive capacity of small hexaploid topodemes invaded by tetraploids, and this may speed up the replacement of hexaploids by tetraploids.

From the few crosses made, no conclusions can be drawn on the relationship of the east Canadian hexaploid to British hexaploids. It is interesting that it is as freely crossable with British tetraploids as are the British hexaploids, but little significance can be placed on this. I believed that on receipt of the Canadian plant I had been told that it was tetraploid, hence it was crossed with British tetraploids. The cross was so successful that it was only when the chromosome number of the progeny was tested and found to be pentaploid that the error was discovered.

The failure of the crosses between British hexaploids and Alaskan C.latisepala suggests that the latter may be quite a distinct hologamodeme (≙ species). Before any definite conclusions are drawn however, much more needs to be known about North American tetraploids and the newly discovered hexaploids.

TABLE 9.9

THE SELF-COMPATIBILITY OF NON-BRITISH PLANTS

2n	Code No.	Species	Locality	Capsules +seed	Capsules -seed	Good seed	Percentage germination	
2x	48.8	C.rotundifolia	East Germany	5	8	+	66	
2x	11.1	C.gieseckiana	Greenland	0	8	0	0	
2x	63.8	C.cochleariifolia	Austria	0	6	0	0	
2x	3.1	C.gieseckiana	East Iceland	0	6	0	0	
4x	3.1	C.gieseckiana	East Iceland	5	1	+	+	
4x	24.4	C.asturica	North Spain	0	9	0	0	
4x	30.7	C.asturica	North Spain	0	3	0	0	
4x	28.7	C.ficarioides	North Spain	12	0	+	14	
4x	61.8	C.scheuchzeri	Austria	0	7	0	0	
4x	12.1	C.intercedens	Lake Superior	0	2	0	0	
6x	21.7	C.rotundifolia	North Spain	6	4	+	86	
6x	97.6	C.gieseckiana	Isle Gaspé, Canada	5	4	+	66	(poor roots)
6x	14.1	C.latisepala	Alaska	2	3	+	37	

SECTION 12 - THE SELF-COMPATIBILITY OF NON-BRITISH PLANTS

The self-compatibility of plants from the British Isles was discussed in Chapter 7 so this seems to be the most appropriate point at which to discuss the self-compatibility of non-British plants. The results are presented in table 9.9.

Considering the results obtained by other works (see Chapter 7) it was very surprising to discover that a diploid C. rotundifolia from East Germany was quite highly self-compatible. Similarly, one of the two tetraploids from Iceland tested was highly self-compatible.

The plant of C. ficarioides from Spain was unique in producing about as many seed as a result of self-pollination as it did after cross-pollination. As explained in Chapter 7, the low percentage germination is misleading, as all the seeds were fully developed and the low figure results from dormancy.

All three non-British hexaploids were fairly self-compatible, producing more seed per capsule on selfing than most British hexaploids. A high proportion of the seed of the Alaskan hexaploid were fully formed but dormant, hence the low percentage germination. The very young seedlings resulting from the selfing of the Canadian hexaploid showed very poor development of the radicle. This suggests that, though selfing is possible, it is not the usual means of reproduction.

The self-compatibility of non-British plants therefore parallels the situation found in the British Isles; most tetraploids being self-incompatible, many of the hexaploids being somewhat self-compatible, but with indications that out-crossing is the norm.

CHAPTER 10 COMPARISON OF C.ROTUNDIFOLIA IN THE BRITISH ISLES WITH FOREIGN MATERIAL OF THIS AND RELATED TAXA

SECTION 1 - INTRODUCTION

In the previous four chapters I have given a detailed account of the cytology, morphology, ecology and reproductive biology of C.rotundifolia in Britain. In this chapter I shall give an account of material collected outwith the British Isles which might yield information leading to a fuller understanding of the species complex in Britain and perhaps in the whole Northern Hemisphere.

In the most recent works on the subsection Heterophylla for all areas of the Northern Hemisphere (Podlech, 1965, 1970, Kovanda 1970, Fedorov 1965, Shetler 1963, Hulten 1968, Böcher 1960, 1966), the following are described therein as very closely related to C.rotundifolia:-

C.polymorpha, C.gjaevskiana, C.intercedens, C.latisepala, C.langsdorffiana, C.asturica, C.wiedmannii (i.e. most of the members of the series Vulgares)

The characters used by the above authors to distinguish between those species are given in table 3.5. Where there are gaps in the table, that particular character has not been used as a differential characteristic for that species. In such cases the character is variable and much as described for C.rotundifolia. In nearly all cases the literature from which the information was taken was concerned with distinguishing between only one, rarely two, of these species and C.rotundifolia itself. Characters which distinguish the other species from one another are rarely given.

It can be seen from the table that the characters are either quantative (e.g. flower size and number), or very difficult to assess unless both extremes are known (e.g. blunt or acute leaf tips, degree and openness of branching). All these species are limited to particular geographical areas (fig.11.1), and it is at least open to suspicion that they may have been geographically defined. In many cases variants of C.rotundifolia will key

out as of one of these species though occurring well outside the range of that species. An example of this is the identification of C.gieseckiana ssp. groenlandica (the name used for Greenland tetraploids) from Britain (see Chapter 3) and Scandinavia (Podlech 1965). That this can give rise to an illogical and unworkable situation is demonstrated by Podlech's description of scattered individual lowland plants from Britain as C.gieseckiana, while other barely distinguishable plants within the same area are named C.rotundifolia. This seems to be the result of using ovary shape as the single key character distinguishing these two species.

This chapter will take the form of a discussion of each of the species studied, beginning with the members of the series Vulgares mentioned above, before going on to consider species belonging to other series of the Heterophylla.

SECTION 2 - FOREIGN MATERIAL OF DIPLOID AND TETRAPLOID C.ROTUNDIFOLIA s.s.

Living specimens of C.rotundifolia s.s. have been obtained from Norway, East and West Germany, Holland and Austria. Diploids and tetraploids were found among these collections.

Diploids

Diploids were received from Dessau in East Germany and Munich in West Germany. The plants of both collections had the paniculate inflorescences and small flowers described as characteristic of lowland continental European diploids by Böcher (1960). Their flowers were rather deeper in colour than those of most British plants.

Tetraploids

Plants grown from seed collected in a Norwegian woodland were virtually indistinguishable from certain British material, that which has rather slender, and bore several flowered stems.

A collection from Wageningen, Holland, was also very similar to some British material, especially that from heaths in the south and east.

The only other tetraploid collections seen came from the Austrian Alps and the Black Forest region of West Germany. Though they clearly belonged to C.rotundifolia s.s. they could immediately be distinguished from the bulk of British specimens by their deeper, more purple, flower colour. The inflorescences were paniculate, and the relatively small flowers were borne on rather thicker pedicels than would be expected on British plants with a similar flower size.

Though some European material is unlike any specimen from Britain, there do not seem to be any marked discontinuities between British and continental plants.

SECTION 3 - C.POLYMORPHA

Although neither herbarium material nor cultivated plants of this taxon have been seen, a few comments are necessary as it has been mentioned in several places in this thesis.

C.polymorpha has recently been accepted as a good species by Podlech (1965) and Fedorov (1957). Kovanda (1970c), however, reduces it to a mountain subspecies of C.rotundifolia. Bielawska (1968) could find few differences between C.polymorpha and mountain plants of C.rotundifolia, and also demonstrated the total interfertility of specimens of the two species. However, though she believed that C.polymorpha might be merely the end of an altitudinal cline in C.rotundifolia, she did not consider that enough information was available on mountain C.rotundifolia to submerge C.polymorpha in C.rotundifolia.

It can be seen from table 3.5 that the differential characters separating C.polymorpha from C.rotundifolia - fewer, larger, flowers on shorter stems - are those characteristics which are usually characteristic of all high altitude and high latitude populations of C.rotundifolia (cf. Laane 1968). C.polymorpha may

therefore be a polyphyletic assemblage of mountain ecodemes derived from neighbouring lowland C.rotundifolia populations. The practice adopted by Kovanda (1970c) is to recognise 'polymorpha' plants as a subspecies of C.rotundifolia, and this appears to be the most satisfactory treatment in our present state of knowledge.

SECTION 4 - TETRAPLOIDS FROM NORTH SPAIN - C.ASTURICA AND C.WIEDMANNII

In northern Spain the tetraploids in the central Cantabrian Mountains are found in the gorges and high rocky places. They are now isolated from tetraploids of C.rotundifolia by the warmer drier lowlands surrounding their habitats.

The area studied was the Picos de Europa and the narrow strip of land between these mountains and the Bay of Biscay. The plants were found primarily in the gorges of the Rio Deva and the Rio Cares and in the mountains above Covadonga and Los Lagos towards Pena Santa. They appear to be more or less obligately saxicolous, occurring only in rock crevices, on very narrow rock ledges, or occasionally among rock detritus carrying a very sparse vegetation. Even in cultivation the plants are only very weakly rhizomatous. Below about 1000m they were confined to the gorges. 1000m is the altitude of Los Lagos, and about the lower limit of the beech (Fagus sylvatica)cloud forest. Only above this altitude in the moister and cooler regions of the mountains did the Campanulas occur in more exposed situations. The tetraploids thus seem to be very intolerant of competition and to be confined to cool moist environments.

These tetraploids have recently been described as two new species endemic in northern Spain (Podlech 1970).

The difference between these plants and almost all plants of C.rotundifolia are the total glabrousness and strong patent branching of the north Spanish populations. Also, their flowers are of a deeper, more

violet colour than any of the C.rotundifolia s.s. specimens seen in the wild or in cultivation. These topodemes are sufficiently morphologically differentiated to be distinguished by the character mentioned above from almost all specimens of C.rotundifolia s.s.. Although they are interfertile with C.rotundifolia (Chapter 9) they are sufficiently morphologically and geographically distinct that I consider it valid to treat them as at least one separate species.

Within northern Spain there is considerable variation between different topodemes. Plants in the more lowland gullies (fig.5.16) are weak stemmed and straggling. More upland rock ledge plants have the same general appearance which is produced by trumpet-shaped flowers borne on thin, patently branched stems, but they have a more upright habit and bear all flowers at about the same level. A topodeme from near the summit of one of the highest mountains (2500m) (fig.5.17), while retaining the branching pattern of lower altitude populations, had shorter stems, much rounder basal leaves, blunter-tipped stem leaves, more hemispherical ovaries, rounder based corolla, and lighter coloured flowers. This high altitude population had a very distinctive appearance, but it bore the same morphological relationship to more lowland north Spanish populations that all upland C.rotundifolia (e.g. C.polymorpha) bears to lowland C.rotundifolia.

The characters used by Podlech (l.c.) to distinguish C.wiedmannii from C.asturica are taller growth, fewer stems, larger basal leaves and flowers, and more erect calyx lobes. These I believe to be the very features which would separate a plant grown under shady conditions from one grown in stronger light, although this requires experimental investigation. Both in the wild and in cultivation very small basal and transitional leaves of the C.asturica type are borne at the base of most flowering stems, but an isolated non-flowering rosette at the end of a rhizome branch of the same plant will usually bear large long-stalked leaves of the C.wiedmannii type. I therefore consider

C.wiedmannii and C.asturica to be merely phenoplastodemes of the one gamodeme.

These north Spanish tetraploids very closely related to C.rotundifolia are probably best treated as a single, but variable, species, and by the code of nomenclature the correct name is that of the first described species, C.asturica. However, it must be pointed out that I have not seen the type specimens of these two species, and to do so would be essential before coming to any definite taxonomic conclusion.

SECTION 5 - HEXAPLOIDS FROM NORTH SPAIN

In addition to the tetraploids, two hexaploid plants of C.rotundifolia s.l. were collected in north Spain. Unlike the glabrous tetraploids, they were hairy, and in fact had the longest hairs of any specimen of the series Vulgares that I have seen. The two plants varied considerably from one another (figs. 10.1 and 10.2). One (21.7.A) had stout stems, small flowers and a hemispherical ovary, while the other (21.7.B) bore larger flowers with patent corolla lobes and a conical ovary. This latter plant was characterised by a peculiar recurvature of the tip of every linear stem leaf (fig. 5.6), a feature not noticed in any other plant.

The two hexaploid plants were taken from a very sparse population in an Erica vagans - Genista hispanica heath. This was a warm dry habitat on a fairly steep hillside with a southern exposure. The soil was a shallow rendzina overlying limestone (pH 6.7 and 7.2). Such a warm dry habitat appears to be totally unsuitable for the tetraploids.

The ecological distinction between the Spanish tetraploids and hexaploids is thus very marked, and may well prevent hybridisation between the cytodemes. Also, it seems certain that, at least within this small area, they are distinguishable morphologically; the tetraploids being totally glabrous, while the hexaploids are covered with long pilose hairs. There is therefore no question of the hexaploids being assigned to C.asturica.

FIG. 10.1 Spanish hexaploid. Lower altitude plant with stiff stems, small flowers, and hemispherical ovaries.

FIG. 10.2 Spanish hexaploid. Higher altitude plant with larger flower and conical ovaries.

On morphological grounds alone, they could perhaps be placed in C.rotundifolia s.s., but, as will be argued in more detail later, I believe their true affinities might lie with C.gieseckiana. The major objection to this proposal is their obvious thermophily, while C.gieseckiana is an arctic plant.

SECTION 6 - C.LANGSDORFFIANA

C.langsdorffiana is the name given to east Asian harebell populations. Federov uses the greater flower number per stem in C.rotundifolia to distinguish between C.rotundifolia and C.langsdorffiana. However he also describes C.polymorpha as a separate species, distinguishing it from C.langsdorffiana by its broader stem leaves and appressed calyx teeth.

If C.polymorpha is considered conspecific with C.rotundifolia, C.langsdorffiana would be characterised by having few flowered stems, linear stem leaves, and spreading calyx teeth. Although all these features are very variable in C.rotundifolia this character combination is rare, few-flowered mountain and arctic plants usually having broad leaves and appressed calyx lobes. Not having seen any living or dried specimens of C.langsdorffiana, it is impossible for me to come to any conclusions, but it would seem possible that this species is little more than a geographical variant of a polymorphic circumboreal species. It is therefore perhaps in much the same situation as the north Spanish populations, which it may be taxonomically expedient to recognise as one new species - despite interfertility and a very close relationship with other parts of the variable circumboreal tetraploid cytodeme.

SECTION 7 - C.GIESECKIANA AND MATERIAL FROM GREENLAND, ICELAND AND THE ISLE GASPÉ IN CANADA

C.gieseckiana is an arctic species described originally from Greenland. It is distinguished (table 3.5) by its relatively short stout stems each bearing one or a few large (to 30mm) flowers and blunt somewhat spathulate

stem leaves. There are diploid (ssp. gieseckiana) and tetraploid (ssp. groenlandica cytodemes. The diploid is known from Greenland, Svalbard, Mount Washington, and presumed glacial refugia in north Norway (Kovanda 1970c, Löve and Löve 1965, Laane 1968). The two subspecies are not always separable morpholigically (Böcher 1960), and the tetraploid is sometimes said to remain distinct from C.rotundifolia and C.intercedens only in isolation in Greenland, intergrading with more southern tetraploids elsewhere - C.rotundifolia in Scandinavian (Laane 1968, Podlech 1965, but see also Böcher 1966), and C.intercedens in North America (Böcher 1966).

The material studied in this investigation will now be discussed.

(i) Greenland

A single diploid plant has been obtained from Midternaes in south-west Greenland (fig.3.2). As all diploid Greenland material has been named C.gieseckiana ssp. gieseckiana it was considered to be this species. It agrees with descriptions of this taxon in general appearance, each stem bearing a few large flowers in cultivation. However its ovary is somewhat conical and much less markedly hemispherical than was expected from published descriptions (table 3.5).

The most remarkable feature about this plant in comparison with European C.rotundifolia was the large number of transitional and linear - lanceolate leaves borne on the lower and middle parts of the flowering stems. The internodes are relatively uniform and short, while the leaves are relatively uniform and long to about three quarters of the way up the stem. These characteristics are shared by a North American tetraploid topodeme from Lake Superior and a hexaploid topodeme from the Isle Gaspé in the St. Lawrence estuary (fig. 7.11). The Greenland plant has relatively short thick rhizomes. In these leaf and rhizome characteristics it fits very closely the description given by Löve and Löve (1965) of the Mount Washington diploids, which they identify with C.gieseckiana ssp. gieseckiana. Their description runs as follows:

> "These diploids are comparatively small, usually less than 10cm. tall, with short, stout rhizomes, and creeping or ascending stems; the basal leaves are few, cordate to ovate or crenate but more usually almost triangular, entire, with long somewhat hairy petioles; the cauline leaves are linear to lanceolate, rarely broader than 1-1.2mm, and reduced in size only just below the flowers" (my underlining).

In European plants this character combination has only been noticed in some of the hexaploids (see Chapter 5). In most European plants the intermodes tend to become progressively longer and the leaves progressively shorter and more bract-like at a much lower level on the flowering stems.

As characters such as those discussed above are subject to great environmental variation, differences may show up clearly only in cultivated plants.

(ii) Iceland

In Iceland the harebell presents interesting taxonomic and distributional problems. Kovanda (1970c) refers to the presence of C.gieseckiana in Iceland, but questions the occurrence of C.rotundifolia, posing the taxonomic problem. The problem of the distribution is why it should be so rare over most of the country while it is so common in the east - total absence outside the east would be much more easily explained.

Morphology

Morphologically the Icelandic harebells are very similar to British mountain tetraploids. They have a few large flowers borne on relatively stout stems. All specimens seen have their leaves and the lower parts of their stems covered in the minute pilose hairs typical of most harebells. No glabrous individuals were found.

Many plants had the very distinct hemispherical ovaries typical of C.gieseckiana. No *topodeme* however consisted entirely of such individuals. Some plants in every *topodeme* had the conical ovaries which taper into the pedicel, typical of C.rotundifolia. This suggests that ovary shape may be under fairly simple genetic control, and is therefore a poor diagnosite character.

All the Icelandic plants examined were tetraploid.

Thus morphological features alone might suggest that Icelandic topodemes are a mixture of both species with intermediates. This however would be a most unsatisfactory conclusion as field observations lead me to believe that all Icelandic plants are likely to belong to the one hologamodeme, intratopodeme variation being as great as intertopodeme variation.

Distribution

The peculiar feature about the distribution of the harebell in Iceland is its rarity throughout most of the country while being so common in the east and north (Grøntved 1942). If it were present only in the east the distribution could perhaps be interpreted as the result of an inability to spread across geographical barriers. However, it does occur in widely scattered localities throughout the country from which it seems to be incapable of spreading.

If the harebell were native only in east and north Iceland, it could be a relatively recent newcomer from Scandinavia or the British Isles. In this it might be similar to Trientalis europea and Alchemilla faeroensis which are confined to east Iceland and only otherwise occur in Europe. These species are absent from Greenland and North America.

I consider it very unlikely that the Icelandic harebell has come from the British Isles, as the north-western areas of the British Isles nearest to Iceland are inhabited by hexaploids (2n=102), while the Icelandic plants are tetraploid (2n=68). They could perhaps have come from Scandinavia, which is inhabited by tetraploids, via the North Atlantic land bridge (Böcher 1960). If this interpretation (i.e. native only in east and north) were correct, the scattered localities outside east and north Iceland could not be considered as relict topodemes. Instead they would be seen as introductions, brought about either through the agency of man, or such seed-eating birds as the snow bunting which migrate over long distances. However, the introduction of a single, self-sterile, genotype (most tetraploids are totally self-sterile) would not allow

any spread by seed from an original introduction site - and introductions by man or birds would most frequently be of single individuals.

The existence at Gilsbakki (an isolated locality in west Iceland) of three *topodemes* separated by several hundred metres therefore argues against this above interpretation and in favour of at least this *topodeme* being relict.

Outside east and north Iceland the harebell only occurs in scattered localities and only in the lowlands. Einarsson (pers.comm.) has suggested that many of such occurrences are probably introductions, and it is true that the harebell is frequently cultived in gardens in Reykjavik. Jonsson (Director, Botanical Gardens, Reykjavik, pers.comm.) reports that many people moving from the east to other parts of Iceland frequently take with them native plants of the harebell for their new gardens. However, Jonsson considers a plant growing in the Reykjavik Botanic Gardens originating from Dyrafjördur in the north-west Peninsula to be from a native locality.

As mentioned above, I also consider a specimen collected at Gilsbakki, near Husafell, to be native. It grew on a stream-bank in native vegetation in an improved pasture in which the improvement had probably been confined to fertilisation. In the same area the harebell was reported (Magnusson - farmer of Gilsbakki, pers.comm.) to have been seen within the last ten years in a river gorge and in an area of birch woodland. The birch wood locality was not visited, but in the gorge site no harebell plants were found. No harebell was seen in cultivation on any of the farms in the area. Indeed the only introduced plants grown were usually shelter belt trees and imported grass seed for posture improvement. Although it is true that such imported seed might include the harebell as a contaminant, the three sites in which the species had been seen were not in pasture. This suggests that they were native occurrences.

Most of the scattered localities are represented by flowering specimens in the Reykjavik Herbarium. However, if the Gilsbakki locality is at all typical,

many of these populations may be very small. At Gilsbakki flowering has not been noticed in any of the three sites for several years, and the only plant found was growing rather poorly on a stream-side, rock ledge. It bore several flowering stems with very small buds, which are unlikely to have had time to develop to flowers, let alone seed, in 1971. As 1971 was the best summer in Iceland for ten years, it is probable that the harebell has not flowered in this locality for many years. Thus, these very small scattered populations may often be in unfavourable habitats, and rarely produce seed. They are also likely to be inbred and therefore genetically weak, and thus be incapable of spreading even though the climate is suitable. If such a population were reduced to a single genotype, as may have happened at Gilsbakki, subsequent spread by seed is likely to be impossible as the tetraploid cytodeme is usually self-sterile.

Löve and Löve (1956) have concluded that Iceland was joined by land bridges to Europe (Britain and Scandinavia) and Greenland in the last (Eem or Ipswichian) interglacial, but has been isolated ever since. They suggest that some species have survived in coastal nunataks since the Pliocene, and that virtually all the native flora has survived in such situations since the last (Eem or Ipswichian) interglacial.

If this interpretation is correct, I consider it most likely that the Icelandic harebell arrived from Scandinavia or Greenland no later than the last interglacial. It must therefore have survived the most recent (Weichselian) glaciation in refugia, primarily in the east and north, from where it has since spread to a limited extent. According to this interpretation the scattered localities throughout all parts of Iceland, except the east and north, could be the result of both periglacial survival and recent introduction, perhaps by both birds and man. It does not seem reasonable to postulate a post-glacial expansion over the whole country followed by massive extinction.

Climatically the east and the northern Eyjafjördur area are not unique. The growing season is relatively long (an important attribute in considering a

late flowering species such as the harebell), but shorter than in the south and south-west. Also the harebell grows and seeds very successfully in cultivation in Reykjavik in the south-west, and there is no obvious reason why it should not spread from its isolated localities in this area.

The east and the Eyjafjördur area are however geologically comparatively old, being composed of Tertiary basalts. Both areas have high mountains rising steeply from fjords. This has been described by Dahl (1946) as the ideal situation for peri-glacial survival because the coastal slopes of the mountains are protected from the inland ice. The south and south-west are, in contrast, very young geologically, and relatively flat.

Only a very few species (e.g. Trientalis europea and Saxifraga nivalis) are common in the east and almost totally absent elsewhere. On the other hand there are several species (e.g. Carex glacialis) which are confined to the mountains round Eyjafjördur and the eastern fjörds . Yet others (e.g. Potentilla stricta, and Phyllodoce caerulea) are wholly confined to the Eyjafjördur area. Thus a considerable number of species have been able to survive in Iceland only in these two areas. Here, not only are geomorphological conditions favourable for periglacial survival, but also, the steep, stepped (as they are composed of successive lava flows) mountains rising directly from the sea to ice capped summits provide a wide range of habitats very close to one another. Extensive populations of harebells have therefore probably been able to survive only in these two areas since the last interglacial.

Taxonomy

The above discussion still leaves unsettled the question of whether Icelandic plants should be referred to C.gieseckiana ssp. groenlandica or C.rotundifolia. If, as suggested above, Icelandic harebells are derived from east Greenland or northern Scandinavian *topodemes*, the answer should perhaps be C.gieseckiana ssp. groenlandica. This would be presuming that, before the

Postglacial (Holozän or Flandrian), northern Scandinavia was occupied by C.gieseckiana (only this species occurs in Greenland today).

From other data it has been concluded that up to the end of the last glaciation arctic areas were occupied by diploid and tetraploid cytodemes of C.gieseckiana. The extent of such topodemes is indicated by the presence of diploids today on Mount Washington, in Greenland, Svalbard, and arctic Norway. At that time C.rotundifolia is believed to have been confined to continental areas of central Europe.

As the diploid ssp. gieseckiana is so widely distributed in arctic areas today, it is almost certain that ssp. gieseckiana, and probably the tetraploid ssp. groenlandica as well, were continuously distributed over the North Atlantic land bridge. It is therefore perhaps rather surprising that the diploid ssp. gieseckiana has not been found in Iceland, which has plenty of fellfield habitats suitable for such an arctic species. On the other hand, Iceland lacks the high arctic refugia such as are present in Greenland and Svalbard, and so the diploid may have become extinct in Iceland during a mild period in the post-glacial or the last interglacial. It is, however, possible that diploids may yet be found in Iceland, and they are most likely to occur in the hills surrounding Eyjafjördur. This area is the refuge of most of Iceland's high arctic species.

Evidence which suggests that the Icelandic harebells came from Scandinavia rather than Greenland is the fact that many Icelandic plants have deep mauve pollen similar to that of many European plants. Böcher (1960) describes all Greenland plants as having cream coloured pollen.

(iii) Isle Gaspé, St. Lawrence estuary, Canada

A living plant and a seed sample collected on the Isle Gaspé were available for study. The Gaspé peninsula is a well known locality for arctic relic plants, the Isle Gaspé being the only site in the area where Campanula uniflora is to be found (Shetler 1963). The C.rotundifolia plants collected

were hexaploid and very striking in appearance (figs. 7.11). The leaf arrangement on the flowering stems is similar to that described for the single Greenland specimen, only the condition is more extreme in the Gaspé material. The stems bear a few large flowers with hemispherical ovaries. Like the sea-cliff hexaploids from the West of Scotland (1.6), it produces no far creeping rhizomes. It thus forms a cluster of shoots, giving a tufted appearance. On morphological grounds this topodeme clearly belongs to C. gieseckiana.

Discussion of C. gieseckiana

The complicated interrelationship between C. rotundifolia and C. gieseckiana discussed by various authors (Böcher 1960, 1966; Löve and Löve 1965; Laane 1968) has been further complicated by some of the new facts which have come to light in this study.

Although the diploids of the two species are quite distinct, within each species the diploid and tetraploid cytodemes cannot be distinguished morphologically in every case. Also the tetraploids are so variable that there are no absolute morphological discontinuities between the two species at this level.

Even though it may be impossible to distinguish them morphologically in every case, it seems useful to retain the name C. gieseckiana ssp gieseckiana for Greenlandic and other arctic diploids. The Greenland tetraploids, which are presumably derived from ssp. gieseckiana can be named C. gieseckiana ssp. groenlandica. This name, however, should not be used for any European (excluding Icelandic) tetraploids in whose origin diploids other than ssp. gieseckiana have almost certainly played a part. I consider this to be the most useful and logical practice, for though some European tetraploids may be almost indistinguishable from ssp. groenlandica, they are probably derived from a European hybrid swarm between tetraploids of the two species, not

directly from Greenland tetraploids.

North American tetraploids may have been derived from the same source as the Greenland plants but some, particularly southern populations, have diverged so markedly (Shetler 1966) that to include them in C.gieseckiana seems inappropriate.

To achieve consistency it therefore seems best to confine the use of C.gieseckiana ssp groenlandica to tetraploids from Greenland, and Iceland.

Western European relic hexaploid populations, and especially the single known Eastern North American hexaploid population, I believe to be derived from C.gieseckiana. At least the American and British; if not the French and Spanish, populations might be described as a new subspecies of C.gieseckiana - perhaps as three new subspecies. Such a practice seems valid and useful in evolutionary terms. It would, however, give rise to difficulties in herbarium taxonomy because of the lack of good qualitative characters to distinguish the British hexaploids from tetraploid C.rotundifolia.

SECTION 8 - C.INTERCEDENS AND PLANTS FROM NEWFOUNDLAND AND THE SHORES OF LAKE SUPERIOR.

In the same way that C.rotundifolia is frequently used to describe most European harebells, C.intercedens is used in North America (Böcher 1966).

Newfoundland

Four plants were obtained from the north east coast of Newfoundland. The one specimen counted proved to be tetraploid. In appearance they were virtually indistinguishable from European tetraploid C.rotundifolia, though in their rather long stem leaves they resembled other American collections and the Greenland plant.

Lake Superior

A seed sample from a topodeme on the shores of Lake Superior gave rise to tetraploid plants. These showed a similar leaf arrangement to that

described for the Greenland diploid and the Isle Gaspé hexaploid. Otherwise these plants were very similar to European C.rotundifolia.

Following Böcher (1966) all eastern North American, and probably all North American, tetraploid harebells would be referred to C.intercedens, although hexaploids as well as diploids from the east should be referred to C.gieseckiana.

Tetraploids from areas near Greenland are virtually identical to C.gieseckiana ssp. groenlandica. Also, morpholigical similarities (flowers concentrated towards the top of the stems) might lead one to believe that, at least in the east, the more southern populations have been derived solely from northern plants. Thus all east North American plants could be regarded as belonging to C.gieseckiana.

However as the tetraploids show a much greater range of variation than the other two cytodemes, other, as yet undescribed, entities may have been involved in their origin. The situation would then be similar to that found in Europe. The use of the name C.intercedens for North American tetraploid harebells would seem to be a useful practice till the evolutionary relationships have been more thoroughly worked out.

C.latisepala (fig.3.5)

Hultén (1968) quotes Shetler as stating that as one moves further west along the Pacific coast of Alaska the harebells become much more lax in habit, eventually being decumbent to pendant, with broadly lanceolate to ovate stem leaves and large flowers. Shetler therefore interprets the situation as a cline, leading to an extreme variant which Hultén has named C.latisepala. All the plants which had been examined are reported to have been tetraploid.

Gadella (1964) reports a hexaploid count from a seed sample collected by Hultén in Alaska. Gadella's plants of this sample behaved differently from

all his other collections in not flowering in their first year, so he passed no comment on their identity beyond stating that they belonged to C.rotundifolia s.l or a related species. Kovanda (1970a), without quoting the source of his information, mentions the presence of hexaploid C.heterodoxa Vest. in Alaska. This taxon seems to have been accepted as more or less synonymous with C.latisepala by Böcher (1960), so it is possible that Kovanda may be quoting Gadella's count.

Like Gadella, I have obtained seed collected in the wild in Alaska by Eultén which has proved to be hexaploid. As the seed sample is labelled "60" it was probably collected in 1960, and may be part of the same collection as that reported on by Gadella in 1964. My plants possess all the extreme features of C.latisepala, and are quite unlike any of the other species or variants of the complex that I have seen.

It may therefore be tentatively suggested that the most extreme hexaploid variations of the complex in Alaska could be referred to C.latisepala, though whether such plants are always distinguishable from tetraploids in the same area will have to be resolved by further study. It is interesting to note that the situation in Alaska may parallel that in Britain - the most extreme variants being hexaploid, but being approached in appearance by the tetraploids in the areas where the two cytodemes meet.

SECTION 9 - NOTES ON SPECIES OF THE SUBSECTION HETEROPHYLLA WHICH BELONG TO SERIES OTHER THAN THE VULGARES

Specimens of several species of the section Heterophylla belonging to series other than the Vulgares were obtained for comparison with C.rotundifolia. The species studied were the diploids C.cochlearifolia and C.mairei, and the tetraploids C.scheuchzeri and C.ficarioides. Unlike the species discussed in the last chapter, the above few species seem to be usually quite distinct and rarely confused with C.rotundifolia s.s. However, intermediates between

C.scheuchzeri and C.rotundifolia s.s. are said to occur (Böcher 1963, Gadella 1964, p.97, Podlech 1965, p.61), and the two species certainly hybridise easily (Chapter 9). Gene transfer from diploid C.cochleariifolia to tetraploid C.rotundifolia has been demonstrated experimentally by Bielawska (1964), but there is no evidence that this occurs in the wild.

I have shown that, in cultivation, C.cochleariifolia has limited interfertility with diploid C.rotundifolia and that tetraploid C.ficarioides and C.scheuchzeri are freely crossable with tetraploid C.rotundifolia (Chapter 9). Despite this, it would seem from the literature that these species are usually quite distinct. On the other hand if hybrids do occur, they may be so similar to C.rotundifolia that they have escaped detection.

C.cochleariifolia (2n=34) (fig.3.1)

After diploid C.rotundifolia, C.cochlearifolia is the most widespread diploid of the subsection Heterophylla. It occurs on the main mountain ranges of Central Europe but is absent from Greece, Scandinavia and Great Britain. It is said to be a highly polymorphic species (Gadella 1964).

In the herbarium of the Royal Botanic Gardens in Edinburgh there is an undated specimen of C.cochleariifolia (confirmed by D. Podlech) from Belford, Northumberland, from the Terras Herbarium. This is, however, unacceptable as a native record as the site is lowland, and C.cochleariifolia is frequently grown in gardens and could easily have become naturalised. Being a strict alpine, rather than an arctic-alpine, it is relatively unlikely to be found native in Britain. On the other hand such alpines as Cherleria sedoides and Homogyne alpina have reached Britain but are absent from the arctic.

C.cochleariifolia is a member of the series Alpicolae. The flower buds are pendant, the petiole margins ciliate, and the persistent sharply dentate rosette leaves have a glossy light-green colour which gives the species a characteristic appearance (fig.3.1). This species is thus distinguished from C.rotundifolia, and most other species, by several qualitative characters.

The single F_1 diploid hybrid, C.rotundifolia (2x) X C.cochleariifolia, which survived was intermediate in morphology. However it was sufficiently similar to C.rotundifolia that it would probably be included in that species if it were discovered in the wild and its origin were unknown, though the flower buds were nodding (fig. 10.3). Thus introgression is theoretically possible (Bielawska 1964), though no intermediate wild specimens have been seen, even from areas where the two species are sympatric.

C.mairei (2n=34) (fig.3.4)

C.mairei is a species endemic to the High Atlas mountains in North Africa. Herbarium specimens of this species bearing ripe capsules were collected from beside irrigation ditches at about 2,100m (7000ft) on the slopes of Toubkal by an expedition from the University of Newcastle in the summer of 1971. Toubkal (4168m) is the highest peak in the Atlas Mountains. The specimens agreed most closely with Quezel's (1954) var.atlantica forma elata, having inflorescences about 25cm high, usually one, rarely two or three, flowers per stem, and flowers about 12mm long.

C.mairei is described as being very variable, but is characterised by being stononiferous, strongly heterophyllous, and having erect capsules which open by pores in their upper halves. Its systematic position has been much disputed, for though strongly resembling the C.rotundifolia group (susect Heterophylla) in general appearance, its capsules dehisce apically - a key character of the section Rapunculus.

Quézel (l.c) records how C.mairei was first described in 1921 as the var. atlantica of C.herminii, a south Iberian species which is more or less isophyllous, has capsules opening by basal pores, and 2n=32. De Candolle placed C.herminii close to C.rapunculus, but Cabellero, considered that its true affinities lay with C.rotundifolia, and Quézel supports this assertion.

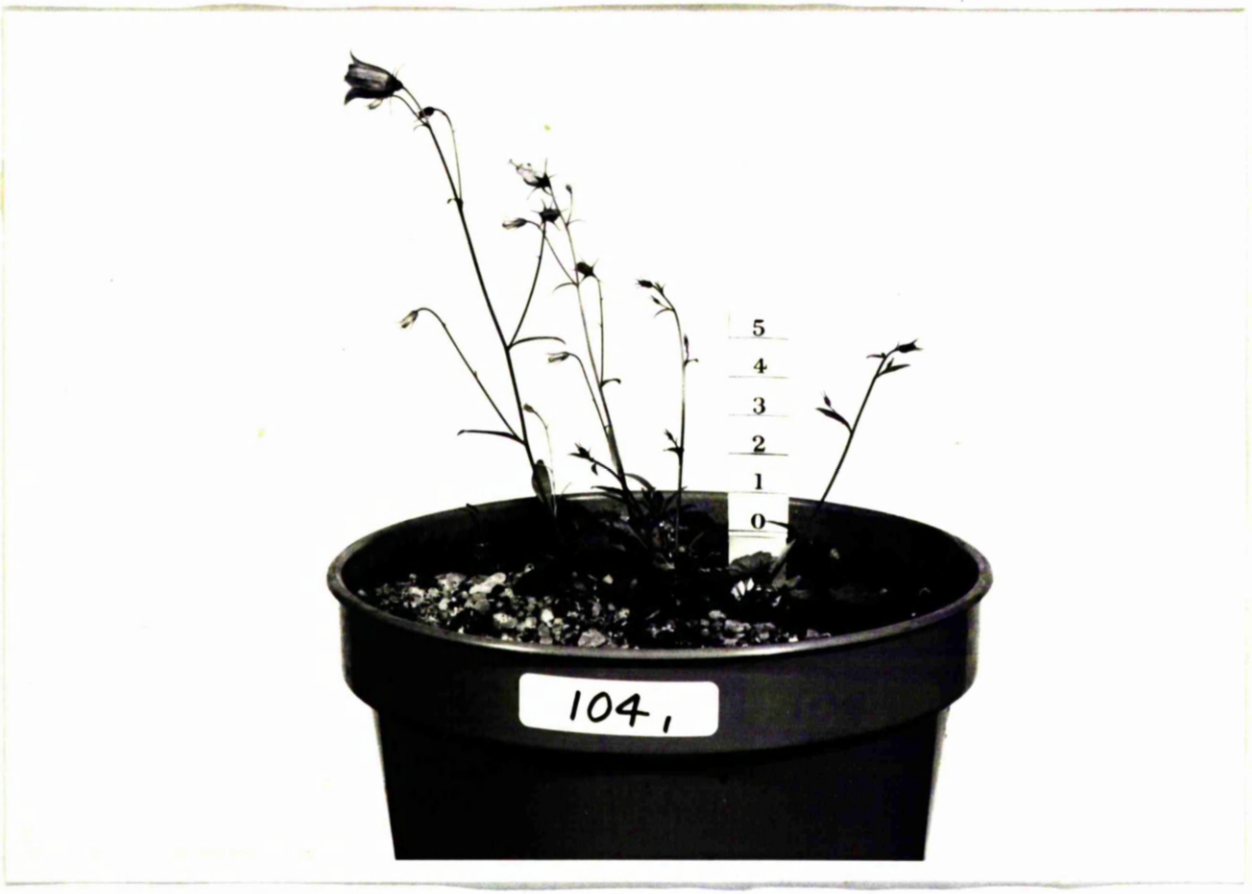


FIG. 10.3 Diploid offspring of cross between diploid C.rotundifolia and C.cochleariifolia.

Because of the apical dehiscence of the capsules and his count of 2n=16, Quézel places C.mairei in the section Rapunculus, and suggests that its affinities are with the C.persicifolia-C.carpatica group of species. Thus, despite a remarkably close morphological resemblance to C.herminnii and C.rotundifolia, which he attributes to convergence, Quézel concludes that C.mairei is only distantly related to these two species.

Gadella (1964) demonstrates that the use of the key characters of position of capsule dehiscence and presence or absence of calyx appendages results in an unnatural classification.

He thus separates C.persicifolia (2n=16, long chromosomes) from C.carpatica (2n=34, short chromosomes), though both species have apical dehiscence. C.persicifolia he places in his Group I (table 3.4) (x=8, long chromosomes). C.carpatica is put in Group VII (x=15, 17 and short chromosomes but including species with 2n=32 and short chromosomes such as C.herminii and C.isophylla whose chromosome number is presumed to have arisen by the loss of one pair from plants with 2n=34). C.mairei is placed in Group I with C.persicifolia largely on the basis of Quézel's count of 2n=16.

On seeing C.mairei I was immediately struck by its close resemblence to C.rotundifolia s.l. My material proved to have 2n=34, which is at variance with Quézel's count, and reopens the question of its systematic position. This is especially so since Gadella (1964) believes chromosome numbers and size to be two of the most reliable indicators of relationship within the genus Campanula. As C.mairei is a very variable species, it is quite likely that it might vary cytologically as well. However, if C.mairei were proven to possess cytodemes with 2n=16 and 2n=34, it would be quite unique in the genus Campanula in which virtually the only type of intraspecific cytological variation known is polyploidy (Gadella 1964). There is a single recorded exception from the wild (Böcher 1963). These however are known or presumed inter-cytodeme hybrids (see also chapter 9).

This cytological observation might of course call into question my identification of the material received as C.mairei. However, the material keys out unequivocally as C.mairei and agrees perfectly with the description given. The only other heterophylleus North African Campanula species, C.jurjurensis 2n=102 and C.hispanica 2n=34, 68, are well recognised members of the subsection Heterophylla and have capsules which dehisce basally. I therefore believe my identification to be accurate and Quézel's chromosome count doubtful. If Quézel's count is correct it might alternatively suggest that C.mairei is heterogeneous and consists of two distinct entities which have not yet been distinguished.

In the light of these new observations it would seem that the only objection to classifying C.mairei in the section Heterophylla, where it would appear to belong on general morphological grounds, is the apical dehiscence of the capsules. Kovanda (1970a) describes how some of the most primitive diploid members of the series Saxicolae of the Section Heterophylla have erect capsules with basal dehiscence, such that the seeds simply fall out of the capsules on ripening. All other members of the Heterophylla have inverted capsules such that the seed cannot fall out unless the capsule is disturbed.

In the evolution of C.mairei, which has erect capsules, it could be that apical dehiscence has been selected, whereas in all other advanced members of the heterophylla the pendant capsule has been selected as the means of improved efficiency of seed dispersal. There is no a priori reason why similarity in two species in the position of dehiscence of the capsule should be more indicative of evolutionary relationship than the stance of the mature capsule. Indeed, Gadella (1964) has shown that the use of such key characters in the genus Campanula results in an unnatural classification. I therefore believe that C.mairei should be placed in the sub section Heterophylla, but am inadequately acquainted with the species of the sub section to comment on its relationship with individual species.

C.scheuchzeri (2n=68, 102) (fig.3.1). (Only tetraploids seen)

Like C.cochleanifolia, tetraploid C.scheuchzeri occurs as all the main mountain ranges of Central Europe. Apart from tetraploid C.rotundifolia and doubtfully distinct species it is the most widely distributed of the tetraploids.

C.scheuchzeri is a member of the series Lanceolatae defined by Podlech and Kovanda as having nodding buds, ciliate leaf bases, and thickened roots. C.scheuchzeri however lacks thickened roots. It is nevertheless quite distinct from C.rotundifolia (series Vulgares) in its nodding buds and ciliate leaf bases. Austrian specimens cultivated at Glasgow also differed from all the cultivated material of C.rotundifolia in general appearance (fig.3.1). The individual components giving rise to this were:ß

1) Shortly creeping rhizomes resulting in a tufted erect plant;
2) Very dark green foliage;
3) Very wide sinuses at the leaf-petiole junction;
4) Short, few-flowered stems with strong dominance of the leading flower;
5) Deep violet blue flowers.

I therefore believe typical C.scheuchzeri to be a species quite distinct from C.rotundifolia. None of the specimens of C.rotundifolia from areas in which C.scheuchzeri grew showed any signs of introgression with that species, though there is a high degree of interfertility between them (see Chapter 9). F_1 hybrids between the tetraploid cytodemes are intermediate between the parent species, but have erect buds, showing dominance of the C.rotundifolia character. They are vigorous, with no obvious hybrid weakness, and pollen fertile, so it would seem that introgression between the two species is theoretically possible. However, it may well be that there is ecological selection for the pure species.

Bielawska (1968) concludes that introgression has occurred in the Tatra mountains, but the Tatra plants have recently been referred to a separate species C.gelida (Kovanda 1968).

C.ficarioides (2n=68, 102) (fig.3.3) (Only tetraploid specimens seen)

C.ficarioides is usually described as being very closely related to C.scheuchzeri, from which it differs primarily in the presence of thickened roots (Podlech 1965, Kovanda 1970c). It has previously been known only as a hexaploid endemic from the Pyrenees, though the specimens at present in cultivation at Newcastle are tetraploids from the Picos de Europa region of the central Cantabrians in north Spain. The details of the habitat in which the plants were found are given in table 10·1.

As well as having thickened roots, these plants differed from the cultivated specimens of C.scheuchzeri in having very long rhizomes and large numbers of elliptic transitional leaves on the flowering stems. This species thus seems to be quite distinct from both C.rotundifolia and C.scheuchzeri though it is freely crossable with C.rotundifolia (See Chapter 9).

Thus C.cochleariifolia, C.scheuchzeri and C.ficarioides, all members of the Heterophylla, are quite distinct from C.rotundifolia. Though they have been shown to be freely intercrossable with C.rotundifolia in cultivation, it is doubtful if much hybridization occurs in the wild.

The diploid C.cochleariifolia is isolated from diploid C.rotundifolia by the weakness of the hybrids (Stebbins 1958), from tetraploid C.rotundifolia it is isolated by ploidy level, which may only be breached in the direction diploid C.cochleariifolia to tetraploid C.rotundifolia. Tetraploid C.scheuchzeri and C.ficarioides are much more freely interfertile with tetraploid C.rotundifolia than are C.rotundifolia and C.cochleariifolia on the diploid level. This could indicate closer relationship, or could be solely a consequence of the greater intercrossability usually shown at higher ploidy levels.

The other species investigated, C.mairei, has never previously been placed in the Heterophylla, with which I believe its strongest affinities lie. It differs from all other species of this subsection in possessing capsules which dehisce by apical values.

TABLE 10.1. HABITAT OF C.FICARIOIDES 2n=68 COLLECTED IN NORTH SPAIN

Habitat: Very dry, crumbling, vertically bedded shale on exposed hillock at summit of pass. Very open vegetation.

Surrounding vegetation: *Erica vagans* heath on deeper soil, *Sarothamnus scoparius* scrub with *Asphodelus* in a sheltered gully.

Locality: Peurta St. Glorio, south west of Potes, Oviedo, North Spain.

Altitude: 1500m (5000ft)

Soil description: p.H. 5.4, crumbling shale.

Associated species:

Festuca rubra	Taraxacum officinalis agg.
Rumex acetosella	Teesdaliopsis conferta
Sedum brevifolium	

Notes: An extremely dry exposed mountain habitat shared with other slow-growing alpines.

Another little known species which may bear a somewhat similar relationship to the Heterophylla is C.parryi, an endemic species in the Rocky Mountains in North America. It too, like C.mairei, has erect capsules with apical dehiscence. Löve and Löve (1965) comment that it might have been involved in the origin of North American harebells. I think this unlikely as all these bear a very close relationship to C.rotundifolia, and C.parryi seems to be a rather distinct species.

SECTION 10 - CONCLUSIONS

The study of non-British material of C.rotundifolia and related species, together with the accounts of other workers, has given a much more complete picture of the complex than study of British plants in isolation.

Morphologically and in their geographical distribution the diploid cytodemes of C.rotundifolia and C.gieseckiana are quite distinct entities.

In the areas where the diploids occur, primarily central continental Europe and Greenland respectively, the related tetraploids are virtually indistinguishable from the diploids. Northern areas of Europe, and perhaps Asia, are colonised by tetraploids of intermediate morphology, and in North America there appear to be no discontinuities between typical C.gieseckiana in the north east and markedly different more southerly and westerly plants referred to C.intercedens. North Spanish tetraploids seem to be separable as a single distinct species.

Hexaploids from the British Isles and eastern Canada, though the former are highly variable, are very close to C.gieseckiana. Other hexaploids from Spain, and perhaps from France, are somewhat similar. The Alaskan hexaploid is rather different and should perhaps be referred to another species.

Wild collected material of series other than the Vulgares is distinct from C.rotundifolia ss.

It is believed that C. mairei, a species endemic to the Atlas Mountains in North Africa, is very closely related to the subsection Heterophylla although it differs from all other species of the Heterophylla in possessing capsules with apical dehiscence.

CHAPTER 11 REVIEW OF THE GEOGRAPHICAL EVOLUTIONARY RELATIONSHIPS OF THE CAMPANULA ROTUNDIFOLIA SPECIES GROUP

SECTION 1 - INTRODUCTION

In this concluding chapter I shall commence by reviewing the information available on British material of the C.rotundifolia complex, indicating the areas in which further study would be most profitable. The second and major section of the chapter will deal with the cytogeography of C.rotundifolia and its closest allies throughout the Northern Hemisphere. In the third and final section parallels will be drawn between this complex and other comparable species complexes, and indications will be given as to which areas would repay further study.

SECTION 2 - SUMMARY OF CYTOTAXONOMIC DATA ON BRITISH C.ROTUNDIFOLIA

In the British Isles two cytodemes are widespread, hexaploids occurring primarily in western and northern coastal areas, and tetraploids occupying most of the rest of the country. A few specimens of both cytodemes have been shown to possess B-chromosomes. Two pentaploid plants have been discovered on Ben Lawers, and an aneuploid has been found in Glendaruel in Argyll near a small hexaploid topodeme which is surrounded by tetraploids. The meiosis and breeding potential of these pentaploids and aneuploids require further study.

Most tetraploids appear to be totally self-incompatible, although two somewhat self-compatible plants have been found. Most hexaploids, on the other hand, seem to have a limited degree of self-compatibility. A survey of the breeding behaviour of a large number of genotypes from a range of habitats would be a most interesting project.

Specimens of the two cytodemes cannot always be distinguished morphologically and both are highly variable. Much of this variation is ecotypic, and

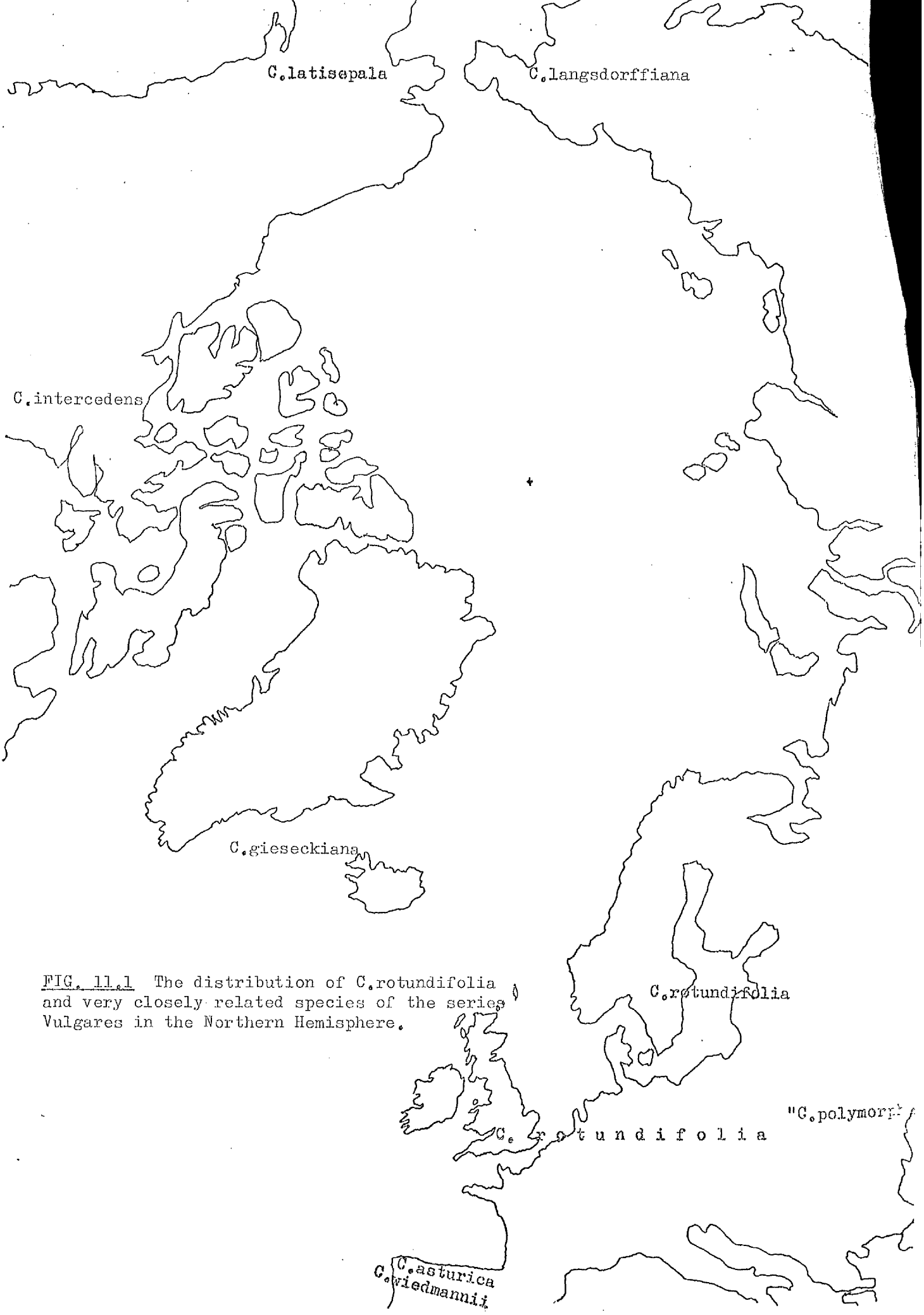


FIG. 11.1 The distribution of C.rotundifolia and very closely related species of the series Vulgares in the Northern Hemisphere.

characteristic ecogenodemes occur in particular habitats. The short stiff exposed cliff variants are particularly striking, though there are also marked morphological differences which appear to be correlated with latitudes and altitude. Much further work is required to gain a fuller understanding of this morphological genecological differentiation. Cultivation experiments to investigate the physiological genecological differentiation with respect to such factors as temperature, soil pH, and daylength would also yield interesting results.

The lack of characters which could distinguish between the two cytodemes suggests that taxonomically they should both be referred to the one species C.rotundifolia. However many, but not all, hexaploids have a very distinctive appearance very close, if not identical, to that of C.giesseckiana.

Having summarised variation patterns in British C.rotundifolia I shall now turn to an examination of C.rotundifolia and closely allied taxa in the Northern Hemisphere, with special attention being paid to Europe and Greenland.

SECTION 3 - CYTOGEOGRAPHY OF C.ROTUNDIFOLIA AND ITS CLOSEST ALLIES

Fig. II.1 shows the world distribution of C.rotundifolia and closely related allopatric species (C.giesseckiana, C.intercedens, C.latisepala, C.langsdorffiana).

As this study has primarily been concerned with C.rotundifolia and the very closely related C.giesseckiana the discussion from now on will be primarily concerned with these two taxa, beginning with the relationship between the cytodemes.

Diploids

As mentioned earlier, diploids occur primarily in areas presumed to have remained unglaciated during the Pleistocene. There seems to be a fair measure of agreement that the diploids fall into two categories (Böcher 1960, Löve and Löve 1965). Firstly there are the arctic diploids which are usually named C.gieseckiana ssp. gieseckiana with headquarters in Greenland and outposts on Mount Washington (Löve and Löve 1965), Spitzbergen (Flovik 1940), Northern Norway (Llane 1968), and perhaps Northern Russia (Gadella 1964). Secondly, there are diploids with a more southern continental distribution usually referred to the diploid cytodeme of C.rotundifolia ss. These are found largely in central Europe, that is in areas which were between the Arctic and Alpine ice sheets. Judging from the published descriptions these two diploid entities appear to be quite distinct, and the few specimens I have cultivated (figs. 3.2, 5.7) seem to confirm this. They are however interfertile (Böcher 1966; Chapter 9) and so presumably closely related.

As they both show disjunct distribution patterns it can be deduced that they are the remnants of two much more widespread populations, one in northern arctic regions and the other in southern continental areas. It is possible that a single pre-glacial circumboreal taxon was split by the development of the ice-sheets into northern and southern halves, which thenceforth diverged into what are virtually two separate allopatric species.

Other closely related diploids exist about which I can make no comment as I have not seen specimens. Firstly there is east Alpine diploid C.rotundifolia quoted by Böcher (1966, p.298) and illustred in Böcher 1960 plate VI. Then there are the other diploid species which might have hybridised with one another and ancestral stocks related to present day diploid C.rotundifolia. Through polyploidy, these may have contributed genomes to tetraploid species, especially the tetraploid cytodeme of C.rotundifolia. Such diploid species are C.witaseckiana C.rhomboidalis, C.hercegovina, C.macrorrhiza, and C.forsythii in Europe

(Böcher 1966) and C.paryii in the Rocky Mountains in North America (Löve and Löve 1965).

Tetraploids

Tetraploids of C.rotundifolia and very closely related taxa have a virtually continuous circumboreal distribution. Only in Greenland and Europe have extensive cytological studies been carried out, although some information is available on North American plants. In this section on the tetraploids the positions in Greenland, Europe, and North America will be discussed before turning to a discussion of their evolution and cytogeography.

Greenland In Greenland the tetraploids are rather similar in appearance to the diploids, although Böcher (1960) considers them sufficiently distinct to be separated as a subspecies - C.gieseckiana ssp. groenlandica. He states that the tetraploids are much more variable than the diploids.

Europe In central Europe the diploid and tetraploid cytodemes of C.rotundifolia are morphologically indistinguishable (Gadella 1964). In other areas of Europe, where the diploids are absent, tetraploids in severe high latitude and high altitude situations tend to resemble Greenland plants, while tetraploids in milder environments resemble the central European plants. There is however a complete intergradation between the extreme morphological forms. For example, on the dry chalklands of southern England the tetraploids resemble the continental diploids. The tetraploids in the north of Britain on the other hand are rather similar to Greenland plants, and, as we have seen (Chapter 3), some have in fact been named C.groenlandica (=C.gieseckiana ssp. groenlandica) by Podlech. Between these two extremes all possible intermediate variants exist along a clinal gradiant from the south to the north of Great Britain (cf. McVean 1953 on Alnus glutinosa)

A similar situation exists in Scandinavia where many northern and mountain populations have been identified as C.gieseckiana ssp. groenlandica (Kovanda 1970c, Laane 1968). Böcher (1966) however disagrees with such identifications,

considering ssp. groenlandica to be confined to Greenland.

North America. In North America the pattern described above is probably repeated. Böcher (1966) in discussing the North East American Harebell (C.intercedens), describes high latitude (Newfoundland) and high altitude (Mount Washington) plants as resembling C.gieseckiana ssp. groenlandica, while more southern harebells are quite distinct from the Greenland plants. On the west coast of North America we have the same situation with northern (and more western in Alaska) plants having larger flowers and broader leaves (Hultén 1968). In this case the extreme end of the cline has been named C.latisepala.

There has been much discussion about the nomenclature of the North American tetraploids (but possibly also including other undetected cytodemes). Löve and Löve (1965) refer northern variants to C.dubia or C.gieseckiana ssp. groenlandica (not making quite clear which they feel is correct) and more southerly plants to C.intercedens. Böcher (1966) effectively invalidates the use of the name C.dubia (and C.pratensis), and uses C.intercedens for all north east American Harebells. Shetler (1963 and 1966), on the other hand, in a study of all the Campanula species of North America, places all harebells in C.rotundifolia, but divides the species up into "four regional morphotypes" which he treats as subspecies.

The origin of the tetraploids

Although there is no experimental evidence to support the assertion, it seems possible on morphological grounds that the two diploid entities (C.gieseckiana ssp gieseckiana in the North Atlantic area from America through Greenland to Scandinavia, and C.rotundifolia in east central Europe) gave rise to autotetraploids within their own distribution ranges. Thus it is probable that at some stage towards the end of the last Ice Age there were diploids and tetraploids of C.gieseckiana in Greenland and northern Scandinavia, and diploids and tetraploids of C.rotundifolia in east central Europe, the taxa being

separated by the remains of the Scandinavian Ice Cap. I suggest that as this ice melted both taxa, and particularly the tetraploid cytodemes, expanded into the newly ice-free areas which were becoming available for colonisation. It is possible that the diploids never met, but I believe that the tetraploids met and hybridised freely [Böcher (1966) asserts that Greenland and central European tetraploids are wholly interfertile]. F_1 hybrids would be virtually a new allotetetraploid, but backcrossing to both parents and crossing among hybrids probably occurred so freely that a hybrid swarm was produced and the distinctions between the taxa broke down. It is likely that the plants of this new hybrid swarm would have been more vigorous than either of their parent taxa, and it seems likely that they rapidly spread throughout most of Europe north of the Alps, giving rise to the variable and successful tetraploid harebell we know today.

Such a hybrid swarm would have hybridised with the autotetraploids wherever they met. Thus the original tetraploid C.gieseckiana would only exist in a pure state today in Greenland and Iceland which are outwith the range of the hybrid swarm, having been cut off from Europe since the last (Eem or Wurm) interglacial (Löve and Löve 1956). Pure autotetraploids of diploid C.rotundifolia might exist in isolated localities in central Europe, but they would be very difficult to detect. Meiotic pairing studies are unlikely to be very informative considering the interfertility of the diploids - cf. Manton (1934, 1937) on Biscutella laevigata.

The gene combinations of C.gieseckiana and diploid C.rotundifolia s.s. were presumably adapted to northern Arctic and continental conditions respectively. It was thus perhaps to be expected that selection within the hybrid swarm would result in tetraploids resembling C.gieseckiana being selected in high latitudes and at high altitudes, and in tetraploids resembling diploid C.rotundifolia being selected in areas with a more continental climate. An original high frequency of the respective autotetraploids in such areas could

be another explanation of the morphological similarities to the ancestral taxa. This, however, is unlikely to be true in the British Isles where the same pattern is found - small flowered plants with paniculate inflorescences in the south and large flowered C.gieseckiana - like plants in the north and in all mountainous areas.

As will be discussed in the next section, I believe the British Isles to have been occupied exclusively by hexaploids towards the end of the last glaciation. As I believe, from a consideration of their present distribution, that the tetraploids entered Britain from the south east after the North Sea had filled, this present British pattern must be the result of natural selection having acted on the hybrid swarm.

Although in this discussion I have considered only the two diploids C.gieseckiana ssp.gieseckiana and diploid C.rotundifolia as the ancestors of the widespread tetraploid European harebell, the other southern European diploids mentioned at the end of the section on diploids could also be involved without necessitating any drastic revision of the above interpretation. If such species contributed genomes, the new tetraploid spreading north would be more heteroyygous than the presumed autotetraploid of diploid C.rotundifolia. or hybrid swarm as assumed above. Much more work is required, particularly on southern European topodemes, to obtain a better understanding of the situation.

I have relatively little information on North American material on which to base any hypothesis, but morphological resemblances suggest that many of the more northern tetraploid topodemes might be derived directly from C.gieseckiana ssp.groenlandica alone. More southern topodemes are somewhat different, but this need not imply the involvement of another diploid. The redundancy present in the presumed autotetraploid ssp.groenlandica would give plenty of scope for the evolution of new variation as it spread southwards. [Ohno (1970) suggests that one result of genetic redundancy is that many

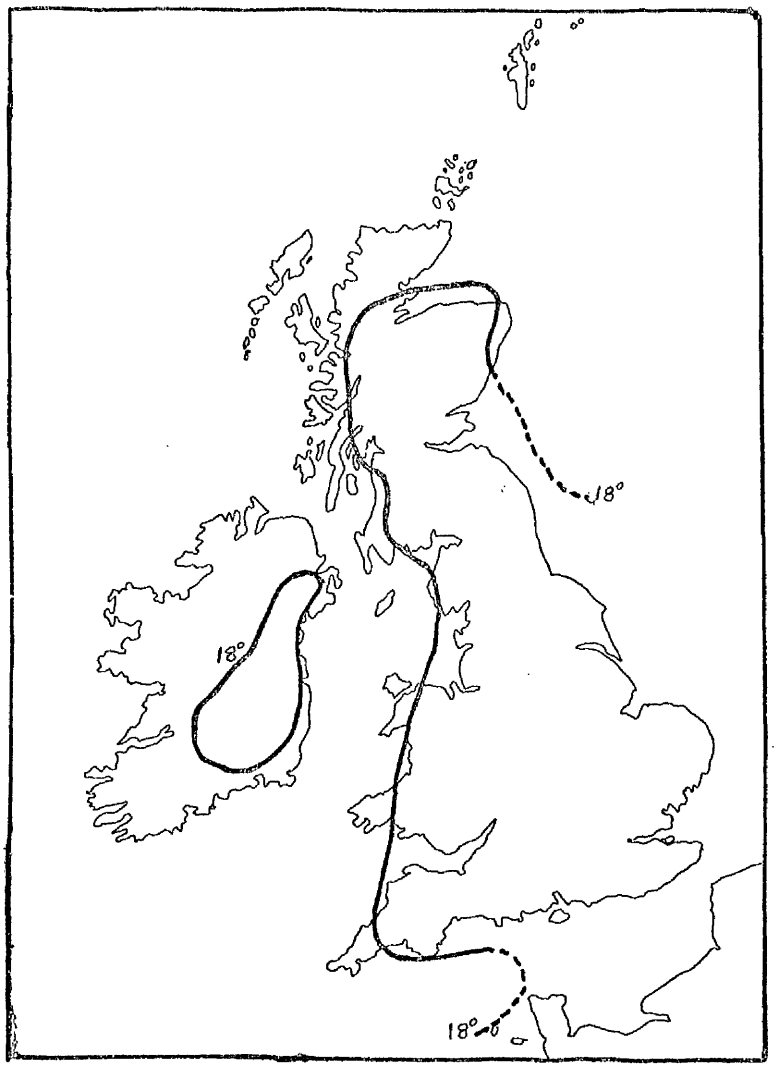


FIG. 11.1 Areas to the west and north of the 18° line have an annual range of mean temperature of less than 18F degrees (after Billham 1938)

mutations survive which would be lethal in organisms lacking gene duplication. These mutant genes are then available to assume new additional functions. Duplication of the genetic material therefore releases an organism from stabalising selection in many vital genes, and by increasing the potential genetic variation available for selection it speeds up the rate of evolutionary change.

On the other hand, other diploids, perhaps extinct or as yet undetected, might have contributed in the formation of the tetraploids.

As Greenland formed part of the North Atlantic land bridge and C. gieseckiana is said to be present in Greenland in a pure form (Böcher 1966) - i.e. with no admixture of genes from any other diploids - east American and European tetraploids may only be related to one another through C. gieseckiana.

The situation in eastern and western North America thus seems to parallel that in north to south transects of Britain or Scandinavia in Europe. There are large-flowered, few-flowered tetraploids in northern regions, and smaller flowered tetraploids with more branched inflorescences in the south (Böcher 1966, Hultén 1968). With little cytological information available, particularly on more northern and western populations, I do not feel able to draw any conclusions concerning the evolution of the North American tetraploids.

Very little information is available (at least to me) on Asian populations. The harebell on this Continent has been named C. langsdorffiana, but its distinctness from harebells in other parts of the world, particularly neighbouring regions of European Russia, appears doubtful (Fedorov 1957).

It would therefore seem that the very common tetraploid cytodeme of C. rotundifolia s.l, at least in Europe, has arisen from two or more diploids by autopolyploidy and allopolyploidy. As the resultant tetraploids were all interfertile, hybridisation and heterosis have presumably led to great variability and vigour. Much more work is however necessary to investigate these hypotheses more fully.

Hexaploids

As mentioned in the introduction, previous hexaploid counts have been so scattered in their distribution that no obvious pattern was discernable. However, with the discovery that western and northern areas of the British Isles are exclusively inhabited by hexaploids, the situation is completely altered.

Within the British Isles the distribution of the hexaploid is that of a northern oceanic species. Its main distribution area is very closely correlated with regions having an annual range of mean temperature of less than 10 Celsius degrees (18F degrees) [(fig.11.2) as taken from Bilham (1938)]. However it also occurs in isolated pockets, often in association with arctic alpine relict species, within the distribution range of the tetraploid cytodeme in areas of the central Highlands and northern England, with an annual range of mean temperature of over 11.1 Celsius degrees (20F degrees). This argues in favour of the hexaploid being a relict taxon which has been replaced from the south-east by the tetraploids wherever its habitats were accessible to that cytodeme. It therefore seems probable that during the last (Weichselian) glaciation, and for at least a short time afterwards, the British Isles were occupied exclusively by hexaploid harebells. Campanula pollen and seeds have been recorded periodically in peat since the late glacial (Godwin 1953, 1956, Pennington 1970, West 1970), and the surrounding vegetation as judged from the pollen diagrams makes the harebell the most probable species (the alternatives C.uniflora, C.patula and C.glomerata are unlikely). This evidence, together with the fact that modern C.rotundifolia and C.gieseckiana inhabit areas very close to the Alpine and Arctic ice sheets, similar climatically to south west Britain during the Ice Age, suggest that the hexaploid could have survived in western areas very close to the Pleistocene ice sheets.

As discussed in Chapter 5, many hexaploid topodemes, and significantly even the more southerly ones from the Lizard and Southern Ireland (fig.5.29), bear a closer resemblance to Greenland C.gieseckiana than to southern British and continental tetraploids. Most hexaploids have the stout stems bearing few large flowers with large but short and broad ovaries, and also the relatively wider, blunter tipped, upper stem leaves of C.gieseckiana. It is also interesting that many, including the southern British, hexaploids have the relatively short stout rhizomes described by Löve and Löve (1965) as characterising the diploid ssp.gieseckiana.

It therefore seems likely that these hexaploids are derived solely from C.gieseckiana, having no admixture of genes from continental C.rotundifolia ss. The most probable mode of origin of such a hexaploid is by chromosome doubling following hybridisation between diploid and tetraploid plants, as suggested by Gadella (1964) for an Alaskan hexaploid.

It is perhaps of some significance that hexaploids have been found in the most oceanic part of northern Spain in the same area as such species as:

> Erica ciliaris, E.vagans, E.mackaiana, Daboecia cantabrica, Pinguicula grandiflora and Arbutus unedo,

which are common to both this area and Ireland.

These hexaploids have many of the features which link their British counterparts with C.gieseckiana and they are quite different from the tetraploids of the surrounding area. It might also be of significance that they occur on the open slopes of the coastal foothills rather than in the higher mountains of the Picos de Europa. They may therefore be in a habitat which remained unglaciated throughout the Ice Age. Their apparent preference for a warm dry habitat is perhaps unexpected, but the very thin rendzina soil gives relative freedom from competition. Associated species in the Erica vagans - Genista hispanica heath included Antennaria dioica, Anthyllis vulneraria, Aster alpinus, and Globularia cordifolia.

Hexaploids have also been reported from the Massif Central in France by Hubac (1961) and Gadella (1964). From the morphological descriptions given they do not seem to bear much resemblance to C.gieseckiana, except perhaps in possessing transitional leaves (Hubac l.c.). However a number of Lusitanian species do occur in this area.

The only other area in Europe from which hexaploid populations of C.rotundifolia have been reported is Czechoslovakia (Gadella 1964). However, Kovanda (1970b), who has made a special study of Czechoslovak species of the subsection Heterophylla, refers these hexaploids to C.moravica - a species distinguished from C.rotundifolia by several qualitative characters (e.g. papillose ovary, woody capsule).

It is recognised that hexaploids may arise through the funtioning of unreduced gametes in a tetraploid population, or through hybridisation between diploids and tetraploids followed by chromosome doubling. If the hexaploid populations had such a recent origin they would be expected to differ very little morphologically from surrounding tetraploid populations (unless hybridisation between two species was involved). They would also be most likely to occur as small scattered topodemes (as described by Roussi 1965 in Potentilla anserina) in association with tetraploids. The Scottish topodemes 45.6 and 100.6 largely satisfy these criteria, but almost all the other hexaploid topodemes in the British Isles and northern Spain do not - often being morphologically distinct and usually spatially isolated from tetraploids.

It should be pointed out that a hexaploid which had arisen spontaneously in a tetraploid topodeme would almost certainly be interfertile with relict hexaploid plants. Because of the spatial isolation of the cytodemes such hybridisation is unlikely to occur.

As discussed earlier, the east Canadian hexaploid fits perfectly with descriptions of C.gieseckiana, and so is almost certainly derived solely from lower polyploid level cytodemes of that species.

On phytogeographical grounds (the North Atlantic land bridge passed through Iceland and Greenland in which no hexaploids have been found) it is unlikely that the European and American hexaploids have a common origin. The same conclusion would be reached on morphological grounds (see Chapter 10). It thus seems that there may have been a parallel evolution of hexaploids from C.gieseckiana on both sides of the Atlantic.

Too little information is available on the very distinctive Alaskan hexaploid to make any proposals concerning its origin, but in contrast to the opinion put forward by Böcher (1960) I believe it to be quite distinct from C.gieseckiana.

An important feature in considering the cytogeography of members of the C.rotundifolia complex is that they occur largely in natural habitats and their distribution is unlikely to be much affected by man's activities. In this it resembles the Biscutalla laevigata complex (Manton 1934, 1937), and is in contrast to the Anthoxanthum odoratum complex (Hedberg 1967).

Summary of cytogeographical conclusions regarding Europe

It is postulated that at some time during the Ice Age the arctic diploids ancestral to C.gieseckiana ssp gieseckiana gave rise to tetraploids ancestral to ssp.groenlandica. At some stage during or prior to the last glaciation hexaploids arose and spread throughout the Atlantic seaboard of Europe, probably replacing diploids and tetraploids in the north, but perhaps colonising new ground in the south. Thus diploid and tetraploid C.gieseckiana probably became confined in Europe to Scandinavia, the hexaploid occurred throughout the Atlantic seaboard from Iberia to the British Isles, while C.rotundifolia was probably an allopatric species of continental Europe.

As the ice melted towards the end of the last glaciation all these entities would have an initial extention of their ranges. However the meeting of tetraploids of C.gieseckiana and C.rotundifolia somewhere in Eastern Europe led to the creation of the vigorous tetraploid hybrid swarm which soon spread throughout the former glaciated areas and also largely replaced the hexaploid in the west. The hexaploid topodemes in western Britain, north Spain, and probably the Massif Central in France, ~~and~~ are therefore interpreted as the remnants of a once extensively distributed cytodeme of C.gieseckiana. Such a disjunction in distribution in a Lusitanian species is quite common, and is merely an extreme form of the distribution of many species confined to the Atlantic seaboard of Europe (Mathews 1926, Heslop-Harrison 1953).

SECTION 4 - CONCLUDING REMARKS

From the data presented in this thesis it can be seen that the C.rotundifolia complex in northern Europe consists of at least two diploids and a superstructure of tetraploids and hexaploids. All three cytodemes have distinctive geographical distributions which must be taken into account in the formulation of hypotheses about their origins.

Parallels may be drawn between all the situations found in the C.rotundifolia complex and those revealed in other species groups, although it must be stressed that each individual complex has a unique evolutionary history and so must be treated on its own. The postulated autopolyploid origin of the higher polyploid levels finds a parallel in Hedberg's (1961, 1964, 1967, 1969, 1970) work on Anthoxanthum, although Jones (1964) disagrees. The suggestion that although a number of diploids exist, only one or two of these have been involved in the origin of the polyploids is similar to the proposals put forward by Manton (1934, 1937) to account for her findings in the Biscutella laevigata complex. Another feature shared by this group and the C.rotundifolia group is the interfertility of the diploids, and therefore

the unsuitability of genome analysis as a means of investigating relationships. Genome analysis has proved to be a very useful tool in the investigation of many species groups (e.g. Gustaffson and Håkansson (1942) on Rosa, and Walker (1961) on Dryopteris), but the assumptions involved have been highlighted by the work of Riley and Chapman (1958) and Riley (1965). The genetic methods used by Nordenskiöld (1953, 1954, 1957, 1960) in her studies on Phleum pratense might therefore be the best techniques to use in the study of C. rotundifolia. Another interesting parallel is with Dactylis glomerata, in which Stebbins (1971) states that natural selection has brought about the evolution of tetraploid ecogenodemes morphologically very similar to both presumed ancestral diploids.

The extensive approach taken to the work on C. rotundifolia precluded the detailed investigation of the large number of problems which were necessarily revealed. In addition to studies on meiosis and genetical experiments of the type carried out by Nordenskiöld, many genecological, population biology, and hybridisation studies could be undertaken. The very marked ecotypic variation requires genecological investigation. The limited studies undertaken here have revealed many problems in the population biology of the species -- a survey of the breeding system of a large number of topodemes is required, experimental work is necessary on seed germination and seedling establishment, and studies could be undertaken on the extent of vegetative spread and the structure of individual topodemes. Further hybridisations to investigate the interfertility of a wide range of taxa, and of topodemes of each taxon from many localities would be most instructive. Much interesting work could be undertaken in the area of quaternary studies, with attempts being made to identify species, and perhaps even the cytodeme, using such seed and pollen characters as might be revealed by the scaning election microscope.

The studies undertaken in the course of the preparation of this thesis have thus revealed many problems worthy of further research.

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